

A Review of the Recent and Late Cenozoic Calyptraeidae of New Zealand (Mollusca: Gastropoda)

BRUCE A. MARSHALL

Museum of New Zealand Te Papa Tongarewa, P.O. Box 467, Wellington, New Zealand; bruceam@tepapa.govt.nz

Abstract. The New Zealand Recent and Late Cenozoic Calyptraeidae are revised. *Maoricrypta* Finlay, 1926, is reinstated as a genus distinct from *Crepidula* Lamarck, 1799, for New Zealand Recent and Tertiary species with two muscles/scars beside the rim of the septal insertion. *Maoricrypta sodalis*, sp. nov. and *M. kopua*, sp. nov. are described, *M. monoxylo* (Lesson, 1830) is redefined, and *M. youngi* Powell, 1940, is reinstated as distinct from *M. profunda* (Hutton, 1873). New Zealand species with a single (right) muscle/scar are referred to *Grandicrepidula* McLean, 1995. These include a Recent bathyal species *G. collinae*, sp. nov., and the Cenozoic species *Maoricrypta salebrosa* Marwick, 1929, and *Crepidula densistria* Suter, 1917. *Grandicrepidula* is interpreted as a genus rather than a subgenus of *Crepidula*. *Zegalerus* Finlay, 1926, is interpreted as a synonym of *Sigapatella* Lesson, 1830, and two new species of *Sigapatella* are described: *S. ohopeana*, sp. nov. of Middle Pleistocene age (Castlecliffian), and the other Late Pliocene or Early Pleistocene (Nukumaruana) *S. nukumarua*, sp. nov. *Sigapatella crater* (Finlay, 1926) is interpreted as a junior synonym of *S. terraenovae* Peile, 1924.

INTRODUCTION

Calyptraeid gastropods are marine, suspension feeding, protandrous hermaphrodites that brood their young (Werner 1951, 1952, 1953, 1959; Hoagland, 1977). The limpet-shaped shells are distinctive in having an internal shelf or septum, and typically are highly intraspecifically variable in shape, the aperture shape matching contours of preferred substrata, generally rocks or shells. Development may be planktotrophic, lecithotrophic or direct, with great interspecific variation in life history within these developmental modes (Hoagland, 1977; Collin, 2000a, and references therein).

The primary objective of the present contribution is to indicate that *Maoricrypta* and *Grandicrepidula* McLean, 1995, are distinctive and appropriate genus groups for New Zealand species referred to *Crepidula* Lamarck, 1799, by Hoagland (1977), and to indicate some defining characteristics of *Sigapatella* Lesson, 1830, which Bandel & Riedel (1994) interpreted as a synonym of *Calyptraea* Lamarck, 1799. New Zealand Recent calyptraeids are reviewed taxonomically in this light, together with some of the Tertiary taxa. Finally, a key is provided for the New Zealand Recent Calyptraeidae.

Abbreviations and text conventions: MNHN—Muséum National d'Histoire Naturelle, Paris; NMNZ—Museum of New Zealand Te Papa Tongarewa, Wellington; NZGS—Institute of Geological and Nuclear Sciences, Lower Hutt.

MATERIALS AND METHODS

Unless specified, all material examined is at NMNZ (registration numbers preceded by "M.").

Radulae were dissected from buccal masses, cleared of tissue with dilute, cold aqueous solution of potassium hydroxide, washed in distilled water, sonicated, and stored in 80% ethanol prior to dry mounting on carbon tape on aluminium stubs for scanning electron microscopy. Protoconchs were soaked in wetting agent (trisodium phosphate), and sonicated in water to remove extraneous matter, and stored in pure ethanol prior to attachment to stubs using colloidal carbon cement. Images were captured by digital light camera (uncoated specimens), and scanning electron microscopes (gold or carbon/gold/palladium coated specimens). All measurements are in SI units. Magnifications of enlarged images were established using a calibrated microscope optical graticule. Protoconch whorl counting follows Osselaer (1999).

SYSTEMATICS

Superfamily CALYPTRAEOIDEA Lamarck, 1809

Family CALYPTRAEIDAE Lamarck, 1809

Genus *Maoricrypta* Finlay, 1926

Maoricrypta Finlay, 1926:393. Type species (by original designation): *Crepidula costata* G.B. Sowerby I, 1824; Recent, northern New Zealand.

Zeaecrypta Finlay, 1926:393. Type species (by original designation): *Calyptraea monoxylo* Lesson, 1830; Recent, New Zealand. (Introduced as a subgenus of *Maoricrypta*).

Diagnosis: Shell slipper-shaped, large muscle scars beside rim of septal insertion on left and right sides; septal

rim broadly and evenly concave or almost straight, at about right angle to longitudinal axis of shell.

Remarks: Hoagland (1977) presented an unweighted multivariate analysis of 30 crepiduliform calyptraeids incorporating shell size, muscle/muscle scar number, stacking, shell pigment, convexity, preferred substratum, rostration, septal area, septal sulcus, type of larval development, station, and distribution. The result suggested that any group based solely on the number of muscle scars would be polyphyletic. Hoagland (1977) synonymized *Maoricrypta* with *Crepidula* Lamarck, 1799, essentially by stating that the genus was based on geography rather than phylogeny. As she admitted, however, *M. costata* (G.B. Sowerby 1. 1824), *M. "monoxyla"* (not Lesson, 1830 = *M. sodalis* Marshall, sp. nov.), and *M. youngi* Powell, 1940, are distinctive in having large muscle scars beside the rim of the septal insertion on both left and right sides, instead of a single muscle/scar on the right side, or no muscle/scar in either position, as in the great majority of crepiduliform species from outside the New Zealand region, including *C. fornicata* (Linnaeus, 1758), the type species of *Crepidula* (Hoagland, 1977). Hoagland (1977) also admitted that *M. costata* and *M. "monoxyla"* (i.e., *M. sodalis*) seem likely to be related despite pronounced differences in shell morphology, color, type of larval development, and habitat. Other New Zealand species with two muscle scars are *Crypta profunda* Hutton, 1873 (Waipipian?: Late Pliocene—see below), *Crypta turnialis* Bartrum & Powell, 1928 (Opoitian: Early Pliocene), and the stacking form common in Late Miocene (Tongaparutuan) beds in eastern Palliser Bay, which Dell (1952) identified as *Crepidula wilckensi* Finlay, 1924. The muscle scars of *Crypta opuraensis* Bartrum & Powell, 1928 (Opoitian), *Crepidula haliotoidea* Marwick, 1926 (Tongaparutuan: Late Miocene), and *Pilaeopsis radiata* Hutton, 1873 (type locality age Kapitean?: Late Miocene) (? = *Crypta striata* Hutton, 1873) have not been seen because the available specimens are filled with hard matrix, but they are extremely similar to *C. turnialis* and *C. wilckensi* in gross facies and seem likely to be congeneric (it is quite possible that some of them are synonyms). New Zealand taxa with only one (right) muscle scar differ further from those with two in that the septum extends farther anteriorly on the left side than on the right (i.e., obliquely), instead of at about a right angle to the longitudinal axis of the shell: this group includes *Maoricrypta salebrosa* Marwick, 1929 (Dunroonian: Late Oligocene), *Crepidula densistria* Suter, 1917 (Altonian: Early Miocene), and *Grandicrepidula collinae* Marshall, sp. nov., described below. Exceptions are forms of *Maoricrypta monoxyla* that live attached to the exteriors of tightly dextrally coiled gastropods, in which the septum is oblique because the shell twists to right.

Thus New Zealand species fall into two groups that

clearly represent separate phylogenetic radiations, differing from *Crepidula* (s. str.) in the number of muscles/scars beside the rim of the septal insertion, the angle of the septum, and the shape of the septal rim. *Maoricrypta* Finlay, 1926, is available for New Zealand species with two muscles/scars and a simple septum set at about a right angle to the longitudinal axis of the shell. New Zealand species with a single muscle/scar and a simple, oblique septum resemble the type species of *Grandicrepidula* McLean, 1995 (*Crepidula grandis* Middendorf, 1849, Boreal Pacific), and are referred there. Although *Grandicrepidula* was introduced as a subgenus of *Crepidula*, I prefer to allocate it equal rank as a genus beside *Maoricrypta*, pending cladistic analysis of a much wider range of taxa than are discussed here, ideally incorporating molecular data. Incidentally, all nominal Australian crepiduliform species that I have examined have a single muscle/scar and thus evidently belong in *Grandicrepidula*, the exception being *M. immersa* (Angas, 1865), which has two muscle scars and thus probably belongs in *Maoricrypta*.

The only crepiduliform species known to me from outside the New Zealand region with two muscles/scars, other than *M. immersa*, are *Crepidula aduica* G.B. Sowerby I, 1825, and *C. uorrisiarum* Williamson, 1905, from the northeastern Pacific. Whether or not the extra muscle has been derived independently in these species remains to be established. Hoagland (1977) considered that the muscle/s beside the septal insertion (which attach the body to the shell roof) were novel structures that were not derived from the columellar muscle, remnants of which are attached along the anterior edge of the septum (i.e., columella) in some species. This remains to be demonstrated histologically.

Note that *Crepidula haliotoidea* Marwick, 1926, is not a junior homonym of *Crepidula haliotoidea* [sic] G. Fischer, 1807 (lectotype designated by Ivanov & Kantor, 1991), though as indicated by Ivanov et al. (1993), Fischer's name is clearly misspelled in the original publication (Fischer von Waldheim, 1807). *Crepidula haliotoidea* is clearly not referable to *Crepidula*, and is more likely to belong in *Calyptraea* (s. str.).

Hoagland's (1977:365) record of *Crepidula aculeata* (Gmelin, 1791) from New Zealand is obviously based on mislocalized material, as it certainly does not occur in the New Zealand region.

Maoricrypta costata (G.B. Sowerby I, 1824)

(Figures 1, 2, 11, 25, 26, 66)

Crepidula costata Sowerby, 1824, no. 23, pl. 152, fig. 3; Reeve, 1842:29, pl. 143, fig. 3; Reeve, 1859a, *Crepidula* pl. 4, figs. 21a, b; Martens, 1873:28; Sowerby, 1883:67, pl. 452, figs. 113, 114; Suter, 1913:287, pl. 44, figs. 6, 6a; Iredale, 1915:456; Hoagland, 1977:370; Beu & Maxwell, 1990:408; Bandel & Riedel, 1994:341.
Crepidula costata Deshayes, 1830:26; Quoy & Gaimard,

1835:414, pl. 72, figs. 10–12; Deshayes & Milne-Edwards, 1836:644; Hoagland, 1983:2. (All not Sowerby, 1824, nor Morton, 1829).

Crypta costata.—Hutton, 1873a:32; Hutton, 1873b:14; Hutton, 1878:30; Hutton, 1880:87; Hutton, 1883:122, pl. 14, fig. A.

Crepidula (Crypta) aculeata.—Tryon, 1886:129 (in part not Gmelin, 1791), pl. 39, fig. 65 only.

Crepidula aculeata.—Suter, 1904:79 (not Gmelin).

Maoricrypta (Maoricrypta) costata.—Finlay, 1926:393; Powell, 1937:73, pl. 10, fig. 27; Powell, 1946:75, pl. 10, fig. 27; Powell, 1957:99, pl. 10, fig. 27; Powell, 1962:92, pl. 10, fig. 27; Powell, 1976:95, pl. 17, fig. 27; Powell, 1979:149, pl. 30, fig. 13.

Crepidula (Maoricrypta) costata.—Wenz, 1940:904, fig. 2661.

Maoricrypta costata.—Pilkington, 1974:419.

Description: Shell adequately described by Suter (1913:287), and Powell (1979:149). Radula (Figure 66) distinctive among New Zealand *Maoricrypta* species in having narrowly tapered terminal cusps on central and lateral teeth, and relatively large terminal cusps on each lateral tooth.

Type data: *Crepidula costata* Sowerby: 3 “Probable syntypes” BMNH 1993118, the largest of which appears to be the original figured specimen. *Crepidula costata* Deshayes: 3 syntypes MNHN; “Nouvelle-Zélande.”

Other material examined: Fossil—Castlecliff, Wanganui, 5 lots (NMNZ) from unspecified horizons, Middle Pleistocene (Castlecliffian); Ohope (W15/644519), shell-beds below old reservoir in stream at foot of Ohope-Whakatane road, 1970–1971, B. A. Marshall, Castlecliffian (4, M.43129); Te Piki road cutting, between Whangaparaoa and Te Araroa (Y14/561904), 1966–1969, B. A. Marshall, Late Pleistocene (Haweran) (3, M.40118). Recent—ca. 1500 specimens (114 lots NMNZ) from throughout the geographic and bathymetric range.

Distribution (Figure 11): Middle Pleistocene (Castlecliffian) to Recent. Cape Maria van Diemen to as far south as Mahia, North Island, New Zealand, living intertidally to 47 m. Dead shells from as deep as 74 m are probably due to post-mortem transport.

Habitat: Attached to undersides of rocks and on living *Perna canaliculus* (Gmelin, 1791) (Mytilidae) at and below low tide level. Locally on bases of living *Xenophora neozelanica* Suter, 1908 (Xenophoridae), in some cases together with *M. youngi*.

Remarks: This common, well known species is distinctive among Recent crepiduliform calyptraeids from the New Zealand region in its typically strongly radially ribbed shell, pale ribs, and deeply pigmented interspaces.

The oldest specimens examined are from unspecified horizons of Middle Pleistocene age in the Wanganui section, with the earliest recorded occurrence (Fleming,

1953) in the Kaimatira Pumice Sand Formation, Wanganui (Middle Pleistocene). A good growth series from a Nukumaruan (Late Pliocene or Early Pleistocene) shell-bed (deposition depth almost certainly < 50 m) on the north bank of the Mangahao River, south of Mangahao, north Wairarapa (map reference NZMS260, T24/462805), apparently comprises two species, both with radially ribbed forms. The smaller of these species (M.151103, length up to 26 mm) resembles Recent *M. costata* in protoconch (Figure 28) and early teleoconch morphology, and ranges from markedly depressed to highly arched, the majority of specimens having an irregular surface, a few with distinct radial ribs. The largest specimen resembles typical Recent specimens of *M. costata* in overall shape. By comparison, in the larger species (M.42648, length up to 44.5 mm), the start of the first whorl of the protoconch (Figure 29) is more completely covered by the teleoconch, more specimens are radially ribbed, all but one of the shells larger than 14 mm are highly arched (one moderately arched specimen 21 mm long), and the apex becomes strongly offset to the right side as the shell enlarges. The smaller species seems likely to be an early form of *M. costata*. The larger, highly arched species clearly belongs to the form-group that includes the type material of *M. laliotoidea*, *M. radiata* (Hutton, 1873), *M. wilckeusi*, *M. turuialis*, and *M. opuraensis*, the status of most or all of which will be difficult if not impossible to resolve until protoconchs are known (see remarks on *M. youngi*). Fleming (1953:209) recorded what is presumably the same highly arched species (as *M. radiata*) as having its last appearance at several localities in undifferentiated formations of the Kai-Iwi Group, overlying the Kaimatira Pumice Sand Formation (Middle Pleistocene), so it evidently went extinct during the Middle Pleistocene. Calyptraeids have an excellent fossil record in the Wanganui sequence (Fleming, 1953), though potentially highly fruitful analysis of the rich material already available from there (NZGS) is beyond the scope of the present contribution.

Maoricrypta costata has been recorded twice in the literature as occurring in Dunedin Harbour (Pilkington, 1974; Bandel & Riedel, 1994), though I have been unable to acquire material from there for confirmation. Assuming these specimens were correctly identified (and there seems no reason to doubt this), the Dunedin population probably originated from the northern North Island through introduction attached to ship hulls.

None of the specimens labeled as probable syntypes (BMNH) are strictly similar to the original illustration, though there is no reason to doubt that they are conspecific or syntypes. The largest of these specimens is closest to the original illustration, and was the one illustrated by Reeve (1859, pl. 4, figs. 21a, b).

According to Martens (1873), this was the species recorded from New Zealand as “La retorte cannelée” by J. & J. G. Favanne (1780:565), though the accompanying

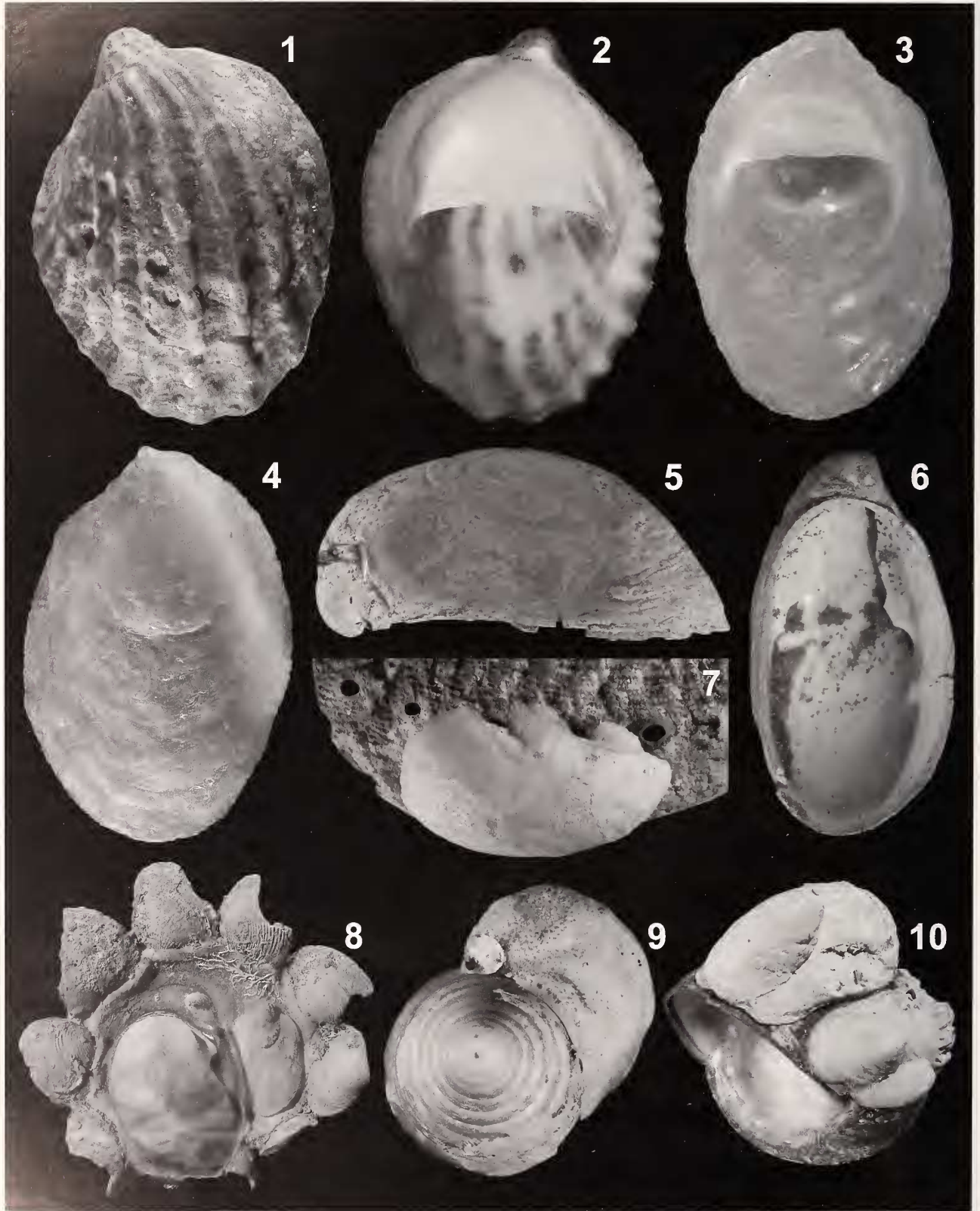


illustration clearly does not represent any species occurring in the New Zealand region. Martens (1873) also stated that *Sigapatella novaezelandiae* was recorded by the Favannes, but again none of the illustrations actually seems to represent it.

Maoricrypta youngi Powell, 1940

(Figures 3, 4, 7, 8, 9, 12, 27, 30, 70)

Crypta contorta.—Hutton, 1873b:14 (not Quoy & Gaimard, 1835; Wanganui record only).

Maoricrypta youngi Powell, 1940:232, pl. 33, figs. 12, 13.

Maoricrypta (Maoricrypta) youngi.—Powell, 1946:75; Powell, 1979:149, pl. 30, figs. 11, 12.

Crepidula youngi.—Hoagland, 1977:394.

Crepidula profunda.—Beu & Maxwell, 1990:259 (in part not Hutton, 1873).

Description: Shell up to 26 mm long, crepiduliform; shape extremely variable (depending on substratum), profile ranging from highly arched and laterally compressed, to weakly convex and broad, apertural plain ranging from more or less flat to concave from side to side or from end to end. Exterior color typically uniform pale yellowish brown, occasional specimens deep yellowish brown, some strongly pigmented specimens with color pattern of irregular radial lines. Protoconch 1.50–2.00 mm long, first 0.6 whorl more or less smooth, 1.00–1.10 mm long, exposed part of start 330–430 μm wide; succeeding patelliform part sculptured with fine, crowded radial grooves. Teleoconch surface texture irregular, variable, no definite sculpture though occasional specimens with sculpture approximately matching that of gastropods to which they are attached; typically weakly twisting to right with increasing growth. Septal rim broadly and evenly concave, more or less at right angle to longitudinal shell axis. Left and right shell muscle scars large, beside insertion points of septal rim. Radula (Figure 70) resembling that of *M. costata* in relatively large size of terminal cusps on central and lateral teeth, but differing in that secondary cusps on these teeth are relatively larger.

Type data: Holotype Auckland Institute and Museum AK 70437; Cape Maria van Diemen, N North Island, New Zealand, beach.

Other material examined: *Fossil*—"Wanganui (U),"



Figure 11. Distribution of *Maoricrypta costata* (G. B. Sowerby I, 1824) off North Island, New Zealand (200 and 1000 m isobaths indicated).

apparently the specimens identified by Hutton (1873b) as *C. contorta* (2, M.27324; personally removed from associated wooden tablet with a type-set label "*Crepidula crepidula* L. (Suter, 1912). (*Crypta contorta* Q. & G. Hutton, 1873. Loc. Wanganui (U))" = Pleistocene. *Recent*—Several hundred specimens (56 lots NMNZ) from throughout the geographic and bathymetric range.

Distribution (Figure 12): Pleistocene and Recent. Off North Island from northern Northland to Cook Strait, New Zealand, living at low tide (Castlepoint) and at 18–88 m.

Habitat: Under peripheral keels of living *Astraea heliotropium* (Martyn, 1784) (off Cape Reinga, 88 m, M.36032; Waimarama, Hawke Bay, 15 m, M.95208; off Rangitikei, 75 m, M.51620). On bases of living *Xeno-*

←

Figures 1–10. Shells of *Maoricrypta* species. Figures 1, 2. *Maoricrypta costata* (G. B. Sowerby I, 1824), Bowentown, Bay of Plenty, sublittoral, length 41.3 mm (M.40049). Figures 3, 4. *Maoricrypta youngi* Powell, 1940, Colville Channel, 44 m, length 16.6 mm (M.35435). Figures 5, 6. *Maoricrypta profunda* (Hutton, 1873), lectotype, length 31 mm (NZGS TM8223). Figure 7. *M. youngi* (length 16.2 mm) *in situ* on living *Halionis virginea* Gmelin, 1791, off Amodeo Bay, Coromandel Peninsula, 12–15 m (M.117792). Figure 8. *M. youngi* (length of larger individual 24.5 mm), *in situ* on base of living *Xenophora neozelanica* Suter, 1908, Colville Channel, 44 m (M.35435). Figure 9. *M. youngi* (length 20.5 mm) *in situ* behind apertural rim of living *Maoricolpus roseus* (Quoy & Gaimard, 1834), off Cape Palliser, 73–183 m (M.9747). Figure 10. *Maoricrypta monoxylla* (Lesson, 1830) (length of largest individual 23.4 mm) *in situ* on living *Turbo smaragdus* Gmelin, 1791, Omokoroa, Tauranga Harbour (M.18671).



Figure 12. Distribution of *Maoricrypta youngi* Powell, 1940 off North Island, New Zealand (200 and 1000 m isobaths indicated).

phora neozelanica Suter, 1908 (off Hen Island, 51–57 m, M.35393; Colville Channel, 44 m, M.35435). On parietal area of pagurid-inhabited shell of *Penion sulcatus* (Lamarck, 1816) (off Bare Island, Napier, 13 m, C. Duffy and A. L. Stewart, M.110966). Beside outer lip rim of living *Maoricolpus roseus* (Quoy & Gaimard, 1834) (off Karaka Bay, Wellington, 18 m, M.44147; off Cape Palliser, 73–183 m, M.9747). On exterior of pagurid-inhabited shell of *Charonia lampas* (Linnaeus, 1758) (off Mahia Peninsula, 55 m, D. W. Gibbs, M.117767). On spire of living *Turbo smaragdus* Gmelin, 1791 (Castlepoint, below lighthouse, rock pool, low tide, J. L. Raven, M.152694). On last half whorl of living adult *Calliostoma (Maurea) granti* (Powell, 1931) (off Pania Reef, Napier, 12 m, D. W. Gibbs, M.117791).

Remarks: *Maoricrypta youngi* is closely similar to *M. monoxylla* in teleoconch morphology, but is immediately distinguishable by the brownish rather than white shell, the whitish instead of yellow animal, and the more strongly convex protoconch. Compared with pale, weakly sculptured forms of *M. costata* (with which it may occur on *Xenophora neozelanica* for example), *M. youngi* differs in having a more paucispiral protoconch, which is at first smooth then crisply radially striate, and the start of the first whorl of which is considerably broader (width of exposed part 330–430 μm , versus 230–270 μm) and partly immersed in the teleoconch.

Maoricrypta youngi is locally common as dead shells in Wellington Harbour sediments (e.g., dredge spoils from Falcon Shoal, off Karaka Bay, M.15633), where, judging from aperture shape, they lived on shells of the gregarious turritellid gastropod *Maoricolpus roseus*, which occurs with them. The only specimens taken alive from Wellington Harbour and Cook Strait were attached outside and close to the apertural rims of living *M. roseus* (Figure 9).

Beu & Maxwell (1990:259) suggested that *M. youngi* may be a synonym of *M. profunda* (Hutton, 1873), but they are certainly specifically distinct, the start of the protoconch of the lectotype of *M. profunda* (Figures 5, 6) being considerably narrower than any Recent specimen of *M. youngi* (width 130 μm , as against 330–430 μm). The lectotype of *Crypta profunda* (NZGS TM 8223, formerly NMNZ M.1634)—here designated to ensure stability should other, potentially specifically distinct syntypes be recognized—has well defined left and right muscle scars beside the septal insertion, and clearly belongs in *Maoricrypta* rather than *Grandicrepidula*. It was relabeled (by R. K. Dell about 1948) “Shakespeare Cliff” and “holotype,” presumably copied from a label on the tablet (no longer extant) to which it had been gummed, presumably during curation by Suter in 1912, who may have guessed at the locality (dimensions are closely accordant with those originally given). When introducing *C. profunda*, Hutton (1873b) recorded as localities “Shakespeare Cliff; Awatere; Motanau (L); Patea; Waitotara; Paparoa, Upper Wanganui; Broken River (U),” and characteristically failed to mention a type specimen or where it was from. The cited localities range in age from Early Miocene to Pleistocene. Unfortunately, in citing only “Wanganui, Petane, Matapiro” (Late Pliocene—Pleistocene) for *C. monoxylla* (with *C. profunda* as a synonym), Hutton (1893) offered no clue by elimination, since material from older horizons was not covered in this particular publication. Judging from the associated matrix of soft, fine, grey sand, the lectotype is unlikely to have come from Broken River (Early Miocene), and seems more likely to have originated from a Pliocene or Pleistocene horizon. There is nothing precisely like it among any of the Nukumaruan or Castlecliffian material examined, so it seems unlikely to be younger than Early Pleistocene. As a matter of fact, the matrix is closely similar to that at Waihi Beach, Hawera (i.e., part of the generalistic “Waitotara” of Hutton = Waipipian: Late Pliocene), as is the state of preservation, so there seems a good possibility that the lectotype is a subadult of the large, smooth species that is common there, which has been identified as *M. wilckensi* (Finlay, 1924) (Laws, 1940).

Maoricrypta monoxylla (Lesson, 1830)

(Figures 10, 17, 19, 20, 35, 67)

Calyptrea (Crepidula) monoxylla Lesson, 1830:391.

Crepidula contorta Quoy & Gaimard, 1835:418, pl. 72, figs.

15, 16; Deshayes & Milne-Edwards, 1836:645; Martens, 1873:28; Hoagland, 1983:2.

Crypta contorta.—Hutton, 1873a:32.

Crypta monoxyla.—Hutton, 1880:87; Hutton, 1883:122, pl. 14, fig. B.

Crypta unguiformis.—Hutton, 1878:30 (not Lamarck, 1822).

Crepidula monoxyla.—Martens, 1873:28; Tryon, 1886:128, pl. 37, figs. 35, 36; Suter, 1904:79; Smith, 1915:81 (in part = *M. sodalis*); Hoagland, 1977:382, fig. 14 (in part = *M. sodalis*).

Crepidula crepidula.—Suter, 1904 (not Linnaeus, 1767):79; Suter, 1913:286, pl. 44, figs. 5, 5a (not Linnaeus, in part = *M. sodalis*); Oliver, 1923:529 (not Linnaeus).

Crepidula (Zeacrypta) monoxyla.—Thiele, 1929:249; Wenz, 1940:904, fig. 2663; Powell, 1979:149 (in part = *M. sodalis*).

Maoricrypta monoxyla.—Morton & Millar, 1968, pl. 17, figs. 7, 7a; Walsby & Morton, 1982:61.

Calyptrea monoxyla.—Hoagland, 1983:4.

NOT *Crepidula monoxyla*.—Harris, 1897:246.

NOT *Maoricrypta monoxyla*.—Pilkington, 1974:421, figs. 6A–D (= *M. sodalis*).

NOT *Crepidula monoxyla*.—Eales, 1923:16, figs. 14, 15 (= *M. sodalis*); Bandel & Riedel, 1994:342 (= *M. sodalis*).

Description: Shell up to 29 mm long, rather thin, dirty white externally, porcellaneous white internally, apertural contour variable (matching substratum: exteriors of living helically coiled gastropod shells and mytilid bivalves), externally moderately to strongly convex. Periostracum thin, smooth, translucent, smooth. Protoconch depressed-patelliform, ovate, 2.5–3.3 mm long, smooth until about 500 µm long, thereafter strongly radially striate; bilaterally strongly symmetrical apart from small, deeply immersed apical fold. Septum externally broadly convex, rim broadly and rather evenly concave. Muscle scars large, subcircular. Teleoconch with fine, crowded, irregular, collabral wrinkles, otherwise no definite sculpture. Animal yellow. Radula (Figure 67) similar to that of *M. costata* though smaller and with a relatively much smaller terminal cusp on each lateral tooth.

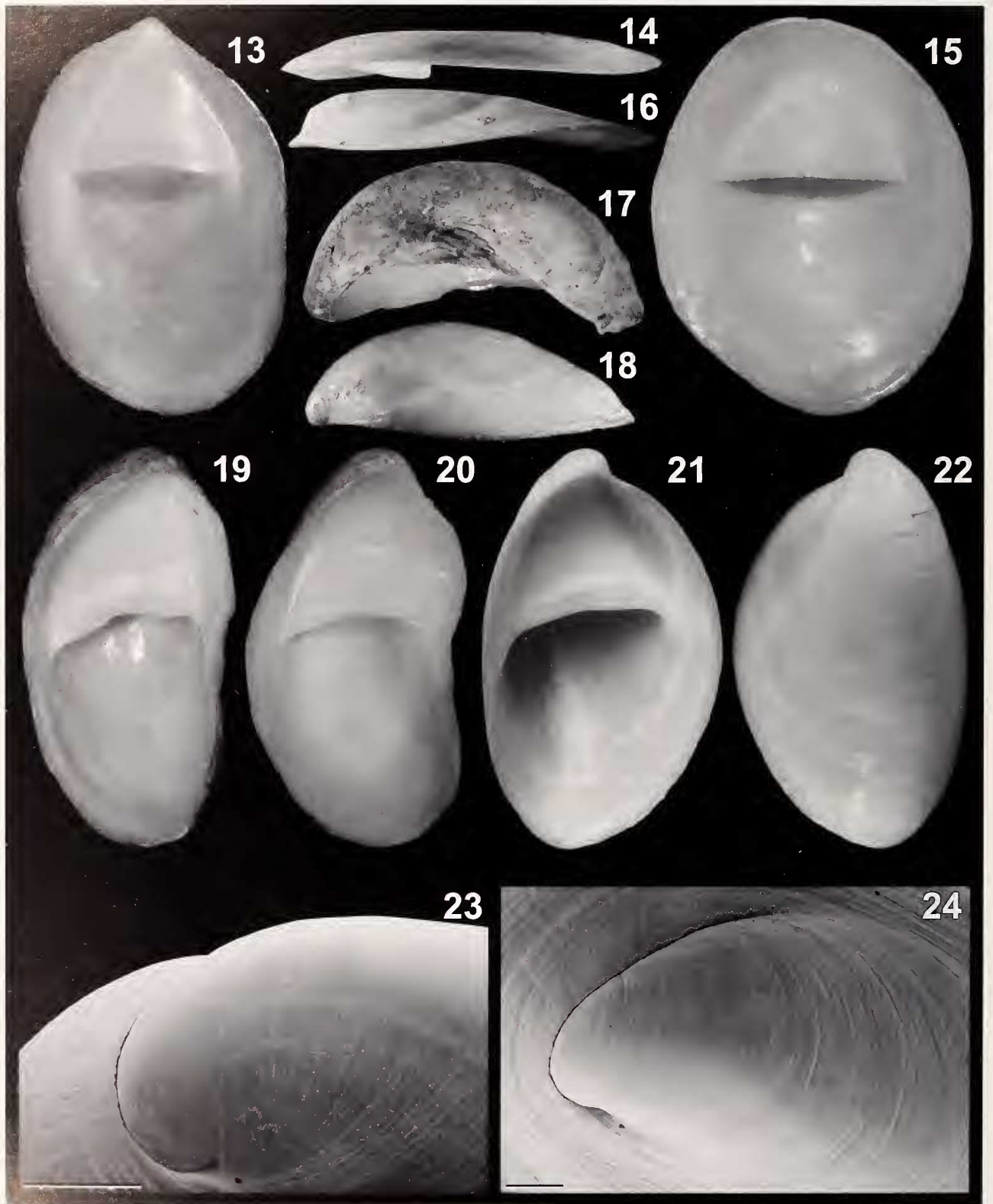
Type data: *Calyptrea monoxyla*: lectotype (this and the following here selected to stabilize the concept of the species in case additional, non-conspecific syntypes are discovered) and paralectotype MNHN; Bay of Islands, North Island, New Zealand (Figures 17, 19). *Crepidula contorta*: lectotype (here selected) and paralectotype MNHN; Bay of Islands (Figure 20).

Other material examined: Parengarenga Harbour, alive on *Turbo smaragdus* Gmelin, 1791, intertidal mudflats, 29 November 1916, W. R. B. Oliver (7, M.16444); off Akatarere Point, Parengarenga Harbour, 4 m, 21 February 1974, R.V. Acheron (2, M.41308); Pukenui wharf, Houhora Harbour, alive, intertidal mudflats, 27 April 1961, W. F. Ponder (4, M.45071); Manawara Bay, Bay of Islands, 2–6 m, 27 November 1971, M.V. *Kokinga* (9, M.40951); Orakawa Bay, Bay of Islands, 4–6 m, 27 November 1971, M.V. *Kokinga* (2, M.154906); Long Beach, Russell, Bay of Islands, alive on *T. smaragdus* Gmelin,

1791, intertidal rocks, 8 December 1911, W. R. B. Oliver (10, M.16438); Oke Bay, Bay of Islands, alive on intertidal *T. smaragdus*, 29 November 1971, R. K. Dell (1, M.42086); Reef Point, Ahipara, alive, intertidal, 24 April 1967, W. F. Ponder (4, M.151210); Reotahi, Whangarei Heads, ex M. Holloway & A. G. Stevenson colln (4, M.90491); Army Bay, Whangaparoa, alive on intertidal *T. smaragdus*, 13 December 1966, W. F. Ponder (2, M.45009); Port Fitzroy, Great Barrier Island, alive on intertidal *Perna canaliculus* (Gmelin, 1791), 10 December 1916, W. R. B. Oliver (1, M.16445); Westmere Reef, Auckland, 14 October 1966, W. F. Ponder (1, M.151208); Narrow Neck Reef, Auckland, alive on *T. smaragdus*, 7 March 1962, W. F. Ponder (2, M.154989); Takapuna Reef, Auckland, alive, intertidal, 7 November 1912, W. R. B. Oliver (8, M.16439); Ponsonby Reef, Auckland, alive, intertidal, 23 August 1914, W. R. B. Oliver (2, 16443); Ponsonby Reef, alive on *Perna canaliculus* from rocks near low tide, 20 April 1912 and 12 October 1912, W. R. B. Oliver (many, M.16450, M.15626); Point Chavalier, Auckland, alive, intertidal, M. Holloway & A. G. Stevenson colln (16, M.90493); Tarakihi Island, Waiheke Island, alive, intertidal, 2 January 1916, W. R. B. Oliver (24, M.16448); Te Puru, Coromandel, beach, September 1958, W. F. Ponder (30, M.18685); off Happy Jack Island, Coromandel, alive on *Buccinulum linea* (Martyn, 1784) and *B. vittatum* (Quoy & Gaimard, 1833), 12–15 m, March 1993, D. W. Gibbs (6, M.117795); off Gannet Rock, Motuwahao Islands, Coromandel, alive on *Haliotis virginea* Gmelin, 1791, *Buccinulum linea*, and *B. vittatum*, 12–15 m, March 1993, D. W. Gibbs (10, M.117792); Tauranga Harbour, alive on *T. smaragdus*, intertidal mudflats, 25 August 1920, W. R. B. Oliver (17, M.16447); Otumoetai, Tauranga Harbour, alive on *T. smaragdus*, intertidal mudflats, 6 April 1995, B. A. Marshall & N. J. Peterson (7, M.119589); Omokoroa, Tauranga Harbour, alive on intertidal *T. smaragdus*, 31 May 1958, W. F. Ponder (30, M.18671); Sulphur Point, Tauranga Harbour, 10 May 1906, W. R. B. Oliver (3, M.16440); W side of Okurei Point, Maketu, alive on *T. smaragdus*, intertidal rocks, 3 March 1996, B. A. Marshall & N. J. Peterson (5, M.130244); Ohiwa Harbour, alive on *T. smaragdus*, intertidal mudflats, April 1967, B. A. Marshall (7, M.40069); Otamaroa, Cape Runaway, alive, intertidal, 8 November 1977, B. A. Marshall (2, M.113581).

Distribution: Northern North Island, as far south as Cape Runaway, New Zealand, taken alive intertidally to 15 m.

Habitat: Living on external surfaces of live *Turbo smaragdus* (Turbinidae), *Buccinulum linea* and *B. vittatum* (Buccinidae), and *Perna canaliculus* (Mytilidae). *Maoricrypta monoxyla* is (or at least was) locally abundant in the Auckland area: a specimen of *Perna canaliculus*, 107 mm long, collected at low tide from Ponsonby Reef, Auckland Harbour, in 1912, was almost completely covered with limpets at all stages of growth (M.16450)—see



reference to this by Oliver (1923, p. 529, as *Crepidula crepidula*).

Remarks: *Maoricrypta monoxyla* traditionally has been interpreted as a species that lives both inside gastropod shells occupied by pagurid crustaceans, and outside living gastropods and bivalves. It transpires that there are three white, more or less smooth-shelled species with superficially similar protoconchs living in association with other mollusks in the New Zealand region, which are characterized by protoconch size and sculpture, animal pigmentation, and habitat. The type specimens of *C. monoxyla* (and its synonym *C. contorta*) represent a species with a yellow animal and a strongly sculptured protoconch that consistently lives on the outside of shells of living gastropods and mussels, intertidally to about 15 m depth off the northern North Island. Although habitat of these type specimens was not recorded, shell morphology is characteristic of specimens living intertidally on *Turbo smaragdus* (Figure 10). The two other species, which typically live within the apertures of helically coiled gastropod shells occupied by pagurids (*never* recorded associated with living mollusks), have whitish animals, more weakly convex or externally concave shells, and more weakly sculptured protoconchs. The common, widely distributed species traditionally interpreted as typical *M. monoxyla* (described herein as *M. sodalis*), lives intertidally to 925 m, and occurs sympatrically both with *M. monoxyla* and a third species (*M. kopua*), which occurs living off the Three Kings Islands and the northeastern North Island at 78–400 m depth.

Maoricrypta monoxyla has direct development and broods its young.

The specimens used by Nelson & Morton (1979) for study of cyclical activity and epithelia renewal in the digestive gland tubules were recorded as having been collected intertidally associated with *Turbo smaragdus*, so evidently represent *M. monoxyla* rather than *M. sodalis*.

Maoricrypta sodalis Marshall, sp. nov.

(Figures 13, 14, 32, 33, 36, 68)

Crypta (Ianacus) unguiformis.—Hutton, 1873a:32 (not Lamarck, 1822).

Crypta unguiformis.—Hutton, 1880:87 (not Lamarck).

Crypta (Ianacus) unguiformis.—Harris, 1897:248 (not Lamarck).

Crepidula monoxyla.—Eales, 1923:16, figs. 14, 15 (not Lesson, 1830); Bandel & Riedel, 1994:342 (not Lesson).

Maoricrypta (Zeacrypta) monoxyla.—Finlay, 1926:393 (not Lesson); Powell, 1937:73, pl. 10, fig. 26 (not Lesson); Powell, 1946:75, pl. 10, fig. 26 (not Lesson); Powell, 1957:99, pl. 10, fig. 26 (not Lesson); Powell, 1962:92, pl. 10, fig. 26 (not Lesson); Powell, 1976:95, pl. 17, fig. 26 (not Lesson); Powell, 1979:149 (in part), pl. 30, fig. 14.

Crepidula monoxyla.—Smith, 1915:81 (in part); Hoagland, 1977:382, fig. 14 (in part).

Crepidula crepidula.—Suter, 1913:286, pl. 44, figs. 5, 5a (not Linnaeus, in part = *M. monoxyla*).

Crepidula (Zeacrypta) monoxyla.—Powell, 1979:149 (in part).

Maoricrypta monoxyla.—Pilkington, 1974:421, figs. 6A–D (not Lesson).

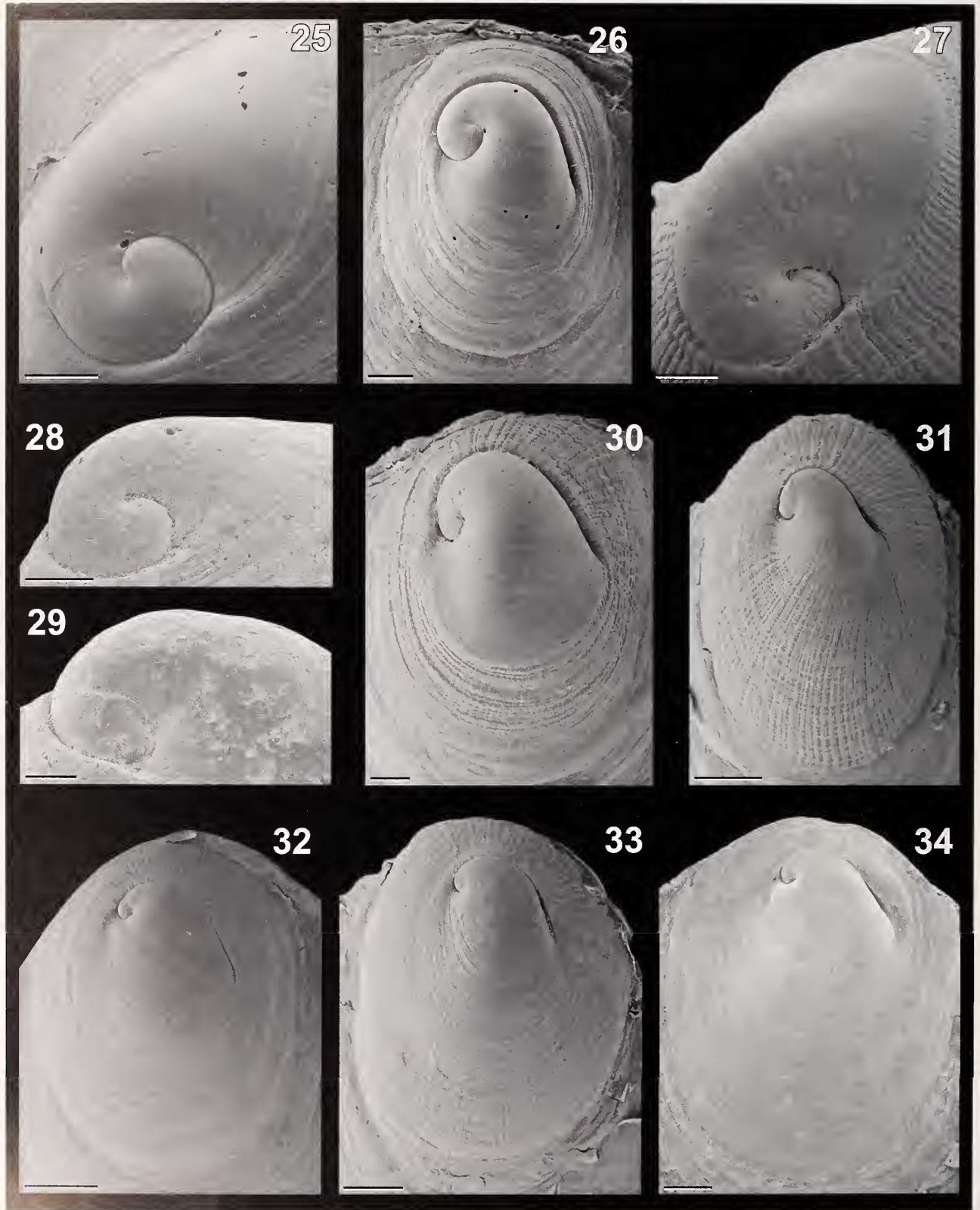
Diagnosis: Shell depressed, smooth, white; septal rim simple, at right angle to longitudinal axis, left and right muscles/scars beside insertion; protoconch 2.8–3.9 mm long, crisply striate. Animal white.

Description: Shell up to 37 mm long, rather thin, uniform white, exterior dull, interior glossy, shape variable (matching substratum: typically interiors of helically coiled gastropod shells occupied by pagurid crustaceans), externally concave or weakly convex. Periostracum thin, smooth, translucent, pale buff, essentially smooth. Protoconch strongly depressed-patelliform, ovate, 2.8–3.9 mm long, smooth until about 1 mm long, thereafter finely and crisply radially striate; bilaterally strongly symmetrical apart from small, deeply immersed apical fold. Septum externally weakly to rather strongly convex, rim broadly and rather evenly concave. Muscle scars large, subcircular. Teleoconch with fine, crowded, irregular, colabral wrinkles, otherwise without definite sculpture. Animal whitish, translucent. Anatomy (Eales, 1923:16—as *Crepidula monoxyla*). Radula (Figure 68) similar to that of *M. monoxyla*.

Type data: Holotype NMNZ M.155092, and paratypes (6, M137270); 36°06.9'S, 174°38.7'E, off Bream Tail, North Island, New Zealand, alive within apertures of gastropod shells occupied by pagurids, 30 m, 25 February 1997, F. V. Ben Gunn. Paratypes: 35°53.6'S, 174°33.7'E, Bream Bay, alive, 22 m, 24 February 1997, F. V. Ben Gunn (4, M.137210); 36°02.4'S, 174°34.7'E, Bream Bay, alive, 16 m, 24 February 1997, F. V. Ben Gunn (2, M.137275); 36°10.1'S, 174°41.9'E, off Te Arai Point,

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Figures 13–24. Shells of *Maoricrypta* and *Grandicrepidula* species. Figures 13, 14. *Maoricrypta sodalis* Marshall, sp. nov., holotype, off Te Arai Point, Northland, length 23.4 mm (M.155092). Figures 15, 16. *Maoricrypta kopua* Marshall, sp. nov., holotype, off Great Barrier Island, 318 m, length 23.7 mm (M.154760). Figures 17, 19. *Maoricrypta monoxyla* (Lesson, 1830), lectotype, Bay of Islands, length 24 mm (MNHN). Figure 20. *Maoricrypta monoxyla*: lectotype of *Crepidula contorta* Quoy & Gaimard, 1835 (a junior synonym), Bay of Islands, length 19.3 mm (MNHN). Figures 18, 21, 22–24. *Grandicrepidula collinae* Marshall sp. nov., holotype, E of Poor Knights Islands, 183–201 m, length 31.8 mm (M.154157). Scale bars = 500 μ m.



alive, 41 m, 25 February 1997, F. V. *Ben Gunn* (14, M.137257); 36°12.2'S, 174°44.7'E, off Te Arai Point, alive, 39 m, 25 February 1997, F. V. *Ben Gunn* (5, M.137289); 36°12.7'S, 174°45.3'E, off Te Arai Point, alive, 37 m, 25 February 1997, F. V. *Ben Gunn* (26, M.137300); 36°13.5'S, 174°45.0'E, off Te Arai Point, alive, 32 m, 25 February 1997, F. V. *Ben Gunn* (10, M.137307); 36°13.9'S, 174°44.5'E, off Te Arai Point, alive, 18 m, 25 February 1997, F. V. *Ben Gunn* (5, M.137318); 37°34.9'S, 177°54.7'E, off Cape Runaway, 27–72 m, R.V. *James Cook*, 3 November 1979 (30, M.65233).

Other material examined: *Fossil*—Landguard Bluff, Wanganui, 24 January 1909, W. R. B. Oliver, Late Pleistocene (Haweran) (1, M.16411); Te Piki road cutting, between Whangaparaoa and Te Araroa (Y14/561904), 1966–1969, B. A. Marshall, Haweran (4, M.40114). *Recent*—> 1000 specimens (194 lots, NMNZ) from throughout the geographic and bathymetric range.

Distribution (Figure 36): Late Pleistocene (Haweran) to Recent. North, South, Stewart, and Snares islands, New Zealand, living intertidally to 925 m.

Habitat: Typically within apertures of helically coiled gastropod shells occupied by pagurids.

Remarks: *Maoricrypta sodalis* is one of the most common and widely distributed calyptraeids in New Zealand, and has the greatest bathymetric range. As indicated above, *M. sodalis* has long been interpreted as part of the variation of *M. monoxyla*, which it resembles in protoconch morphology and in having a white shell, but differs constantly in having a larger, more weakly radially striate protoconch, a flatter or externally concave teleoconch, and a whitish instead of yellow animal.

Maoricrypta sodalis and the species described below are strongly convergent on the North American species *Crepidula plana* Say, 1822, *C. depressa* Say, 1822, and *C. atrasolea* Collin, 2000, in teleoconch morphology and habitat (Collin, 2000b). Development is direct (Pilkington, 1974).

Etymology: Companion (Latin).



Figure 35. Distribution of *Maoricrypta monoxyla* (Lesson, 1830) off North Island, New Zealand (200 and 1000 m isobaths indicated).

Maoricrypta kopua Marshall, sp. nov.

(Figures 15, 16, 34, 64, 69)

Diagnosis: Shell depressed, smooth, white; septal rim simple, at right angle to longitudinal axis, left and right muscles/scars beside insertion; protoconch 3.9–5.0 mm long, weakly striate or smooth. Animal white.

Description: Shell up to 28 mm long, rather thin, uniform white, exterior dull, interior glossy, shape variable (matching substratum: interior of apertures of helically coiled gastropod shells occupied by pagurid crustaceans), typically externally weakly convex. Periostracum thin, smooth, pale buff, essentially smooth. Protoconch depressed-patelliform, ovate, 3.9–5.00 mm long, weakly radial striate or almost smooth, bilaterally strongly sym-

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Figures 25–34. Protoconchs of *Maoricrypta* species. Figures 25, 26. *Maoricrypta costata* (G. B. Sowerby I, 1824), Oke Bay, Bay of Islands, 4–6 m (M.39572). Figures 27, 30. *Maoricrypta youngi* Powell, 1940, Colville Channel, 44 m (M.35435). Figure 28. *Maoricrypta* sp. cf. *costata*, protoconch, bank of Mangahao River, S of Mangahao, Late Pliocene or Early Pleistocene (Nukumaruau) (M.151103). Figure 29. *Maoricrypta* sp. aff. *costata*, protoconch, bank of Mangahao River, S of Mangahao, Late Pliocene or Early Pleistocene (Nukumaruau) (M.42648). Figure 31. *Maoricrypta monoxyla* (Lesson, 1830), protoconch, Tauranga Harbour, intertidal (M.18671). Figure 32. *Maoricrypta sodalis* Marshall, sp. nov., protoconch, Manukau Harbour, intertidal (M.45038). Figure 33. *Maoricrypta sodalis*, protoconch, off Motuhora Island, 72–84 m (M.60600). Figure 34. *Maoricrypta kopua* Marshall, sp. nov., protoconch, N of Three Kings Islands, 128 m (M.151221). Scale bars 25–30 = 200 µm, others = 500 µm.

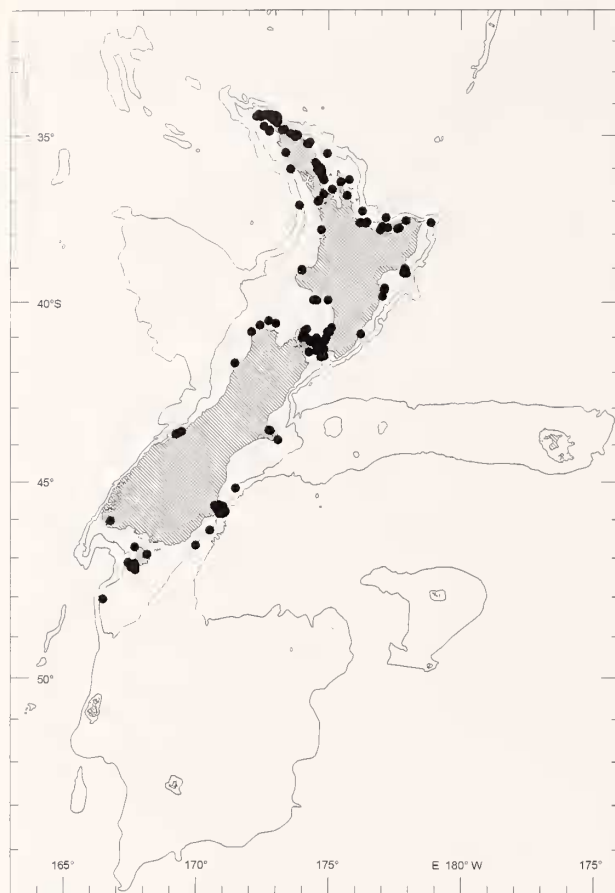


Figure 36. Distribution of *Maoricrypta sodalis* Marshall, sp. nov., off New Zealand (200 and 1000 m isobaths indicated).

metrical apart from small, deeply immersed apical fold. Septum externally broadly convex, rim broadly and rather evenly concave, produced anteriorly farther on left side than on right. Muscle scars large, subcircular. Teleoconch with fine, crowded, irregular, collabral wrinkles, otherwise no definite sculpture. Animal whitish, translucent. Radula (Figure 69) similar to those of *M. monoxyla* and *M. sodalis*.

Type data: Holotype M.154760 and 2 paratypes M.118983, 36°13.8'S, 176°11.6'E, E of Great Barrier Island, N North Island, New Zealand, alive, 318 m, 6 January 1995, F.R.V. *Kaharoa*. Paratypes: 35°33'S, 174°57'E, E of Poor Knights Islands, alive inside aperture of pagurid-occupied gastropod shell, 201–183 m, 14 February 1974, R.V. *Acheron* (3, M.35376); 37°00.95'S, 176°13.99'E, off The Aldermen, alive, 289–292 m, 10 April 1996, F.R.V. *Kaharoa* (2, M.134083); off Mayor Island, alive, 350–400 m, 1991, scampi trawls (3, M.116974).

Other material examined: 33°57.0'S, 171°45.4'E, Middlesex Bank, NW of Three Kings Islands, 98–103 m, 31

January 1981, R.V. *Tangaroa* (2, M.151218); 33°57.0'S, 172°19.0'E, King Bank, N of Three Kings Islands, alive, 128 m, 1 February 1981, R.V. *Tangaroa* (5, M.151221); 33°57.4'S, 172°19.4'E, King Bank, 128–123 m, 1 February 1981, R.V. *Tangaroa* (5, M.151205); 33°58.0'S, 172°30.6'E, 37 km NE of Great Island, Three Kings Islands, 550 m, 25 June 1978, R.V. *Tangaroa* (1, M.151196); 33°59.9'S, 171°45.3'E, Middlesex Bank, 186–196 m, 31 January 1981, R.V. *Tangaroa* (2, M.112787); 34°00'S, 171°55'E, Three Kings Trough, 805 m, 15 July 1962, R.N.Z.F.A. *Tui* (1, M.20816); 34°01'S, 172°07'E, N of Three Kings Islands, 622 m, 18 February 1974, R.V. *Acheron* (1, M.34820); 34°01.2'S, 171°44.4'E, Middlesex Bank, 206–211 m, 31 January 1981, R.V. *Tangaroa* (3, M.151199); 34°01.4'S, 171°45.2'E, Middlesex Bank, 201–216 m, 31 January 1981, R.V. *Tangaroa* (1, M.151197); 34°02.0'S, 171°44.0'E, Middlesex Bank, 246–291 m, 31 January 1981, R.V. *Tangaroa* (5, M.151215); 34°02.1'S, 171°45.8'E, Middlesex Bank, 221–206 m, 31 January 1981, R.V. *Tangaroa* (4, M.151220); Southeast Bay, Great Island, Three Kings Islands, 23 m (possibly dropped from crayfishing boat), 16 February 1986, scuba, F. J. Brook (2, M.109397); 34°05.0'S, 172°24.6'E, 22 km ENE of Great Island, 200 m, 24 June 1978, R.V. *Tangaroa* (1, M.93432); 34°10'S, 172°12'E, off Three Kings Islands, 252 m, 19 February 1974, R.V. *Acheron* (1, M.34092); 34°13.0'S, 172°11.5'E, off Three Kings Islands, 256 m, 19 February 1974, R.V. *Acheron* (1, M.35277); 34°01.8'S, 172°12.0'E, 13 km N of Great Island, 508 m, 23 June 1978, R.V. *Tangaroa* (2, M.151202); 34°14.8'S, 172°13.6'E, SE of Great Island, 173–178 m, 2 February 1981, R.V. *Tangaroa* (2, M.151201); 34°20.0'S, 172°30.0'E, 20 km NW of Cape Maria van Diemen, 100 m, 20 June 1978, R.V. *Tangaroa* (1, M.151200); 34°25.0'S, 172°27.8'E, NW of Cape Reinga, alive, 78 m, 2 February 1981, R.V. *Tangaroa* (1, M.154756); 37°32.8'S, 178°48.7'E, Ranfurly Bank, East Cape, 94 m, 17 January 1979, R.V. *Tangaroa* (2, M.60719); 37°33.1'S, 178°49.5'E, Ranfurly Bank, 94–89 m, 25 January 1979, R.V. *Tangaroa* (5, M.71488); 37°33.4'S, 178°48.3'E, Ranfurly Bank, 106–103 m, 25 January 1979, R.V. *Tangaroa* (4, M.71717); 37°38.5'S, 178°56.4'E, SE slope of Ranfurly Bank, 153–143 m, 22 January 1981, R.V. *Tangaroa* (5, M.151193).

Distribution (Figure 64): Three Kings Islands and northeastern North Island as far south as East Cape (33°57'S–37°38.5'S), New Zealand, 78–805 m; taken alive at 78–400 m (2 shells from 23 m in Southeast Bay, Three Kings Islands may well have been washed from crayfishing boats sheltering there, and it remains to be established whether or not *M. kopua* actually ranges this shallow). Living within apertures of pagurid-inhabited, helically coiled gastropod shells.

Remarks: *Maoricrypta kopua* differs constantly from *M. monoxyla* and *M. sodalis* in having a larger protoconch

(length 3.90–5.00 mm, versus 2.5–3.3 mm and 2.80–3.90 mm, respectively), which is more weakly striate or smooth. Like *M. sodalis*, which also lives within apertures of gastropod shells occupied by pagurids, *M. kopua* differs further from *M. monoxyla* in having a more weakly convex teleoconch and a whitish rather than yellow animal. *Maoricrypta kopua* differs from the southern Australian species *M. immersa* in being consistently uniform white rather than brownish, in having larger muscle scars, and in having a more strongly convex protoconch. *Maoricrypta kopua* and *M. sodalis* are both sympatric and syntopic, although the two species have been taken living together at only one station (off Cape Reinga, 78 m, M.154756, M.151204).

Judging from the large size of the protoconch, larval development is direct as in *M. monoxyla* and *M. sodalis*.

Etymology: Deep water (Maori).

Genus *Grandicrepidula* McLean, 1995

Grandicrepidula McLean, 1995:80. Type species (by original designation): *Crepidula grandis* Middendorf, 1849. Recent, boreal Pacific.

Diagnosis: Shell slipper-shaped, large muscle scar beside rim of septal insertion on right side; septal rim oblique relative to longitudinal axis of shell.

Remarks: McLean (1995) introduced *Grandicrepidula* as a subgenus of *Crepidula* for species with a single muscle/scar (absent in *Crepidula*). Since there is currently no evidence of degree of relatedness, it seems preferable to treat them as distinct genera pending cladistic analysis of the group, as suggested above.

Grandicrepidula collinae Marshall, sp. nov.

(Figures 18, 21, 22–24, 65, 71)

Crepidula sp. Spencer et al. (in prep.).

Diagnosis: Shell arched, smooth, white or axially banded; septal rim simple, oblique relative to longitudinal axis, only right muscle/scar beside insertion; protoconch 4.0–5.6 mm long.

Description: Shell up to 48.5 mm long, rather thin, glossy, strongly convex, strongly oblique, left side of shell compressed, aperture ovate, apertural plain typically twisted in propeller shape (due to common life position on convex outer surface of outer lips, obliquely relative to generating curve, of fusiform gastropods). Exterior uniform white, or white with fine yellowish brown radial lines; interior porcellanous white. Periostracum thin, smooth, pale buff. Protoconch cap-shaped, without coiling suture, smooth apart from fine collabral growth lines, merging almost imperceptibly into teleoconch, of less than half a whorl, 4.0–5.6 mm long (development direct, young brooded). Beak small, appressed to adult margin,

gently inclined to right. Septum deeply inserted, simple, more or less planar, produced anteriorly farther on left side than on right. Muscle scar large, ovate, on right and mostly in front of rim of septum. Teleoconch sculptured with fine collabral growth lines only. Radula: (Figure 71) Central tooth small, subquadrate, cutting area triangular, terminal cusp large, two or three small secondary cusps either side. Lateral teeth broad, cutting area broadly angulate, terminal cusp large, four to six outer and zero to three (typically two) inner secondary cusps. Marginal teeth slender, terminal cusp large, five or six small, slender secondary cusps on inner edge.

Type data: Holotype NMNZ M.154157 and 4 paratypes M.35050; 35°33'S, 174°57'E, off Poor Knights Islands, N North Island, New Zealand, 201–183 m, 14 February 1974, R.V. *Acheron*, alive (brooding) behind outer lip rim of pagurid-inhabited shell of *Alcithoe larochei* Marwick, 1926 (M.35369). Paratypes: 34°49'S, 174°17'E, off Whangaroa, 468–475 m, 24 February 1974, R.V. *Acheron*, alive on inner lip of pagurid-inhabited shell of *Alcithoe larochei* (1, M.33629 on M.33628); 35°33.0'S, 175°12.0'E, off Poor Knights Islands, alive, 390 m, 3 July 1995, F.V. *Albatross*, D. Wrightson (1, M.126985); 36°28.7'S, 173°43.8'E, off Kaipara Harbour, 547–587 m, 12 January 1981, R.V. *Tangaroa*, alive behind outer lip rim of live *Penion* sp. cf. *ornesi* (Powell, 1927) (1, M.74633 on M.74632); 37°00.95'S, 176°13.99'E, off Aldermen Islands, alive, 289–292 m, 10 April 1996, F.R.V. *Kaharoa* (2, M.134084); N of Mayor Island, 380–420 m, December 1987, F.V. *Trinity*, alive behind outer lip rim of pagurid-inhabited shell of *Alcithoe larochei* (2, M.90205); 37°35.31'S, 176°43.07'E, E of Motiti Island, 433 m, 15 January 1995, F.R.V. *Kaharoa*, alive behind outer lip rim of pagurid-inhabited shell of *Alcithoe larochei* (8, M.119046 on M.119044); 37°40.22'S, 177°14.65'E, S of White Island, 205 m, 16 January 1995, F.R.V. *Kaharoa*, alive behind outer lip rim of pagurid-inhabited shell of *Penion cuvierianus* (Powell, 1927) (3, M.119029 on M.119028); 38°08.86'S, 178°45.75'E, off Waipiro Bay, S of East Cape, 211 m, 28 January 1995, F.R.V. *Kaharoa*, alive behind outer lip rim of pagurid-inhabited shell of *Penion cuvierianus* (4, M.119083 on M.119081); 39°29.8'S, 178°10.8'E, E of Cape Kidnappers, 529–568 m, 15 April 1981, F.R.V. *James Cook*, alive behind outer lip rim of live *Alcithoe larochei* (Watson, 1882) (3, M.71976 on M.71977); 39°40.2'S, 177°48.8'E, off Cape Kidnappers, alive, 393 m, 28 February 1998, K. Brady (2, M.147008); 41°50'S, 170°29'E, off Cape Foulwind, 470 m, 23 July 1990, F.V. *Tampen*, alive behind outer lip rim of live *Alcithoe larochei* (2, M.117650 on M.117649); 42°27'S, 170°36'E, off Greymouth, 366 m, 23 November 1970, F.R.V. *James Cook*, alive behind outer lip rim of pagurid-inhabited shell of *Semicassis pyramis* (Lamarck, 1822) (1, M.30773 on M.30771); trawled off Bruce Bay, Westland, 300 m, 10 October 1977, alive

(2, NZGS TM8224); 48°49'S, 167°27'E, SE of The Snares, 560 m, November 1987, F.V. *Chiyo Maru 5*, alive behind outer lip of pagurid-inhabited shell of *Penion benthicola* (Dell, 1956) (2, M.95188 on M.95190).

Other material examined: 35°33'S, 174°57'E, off Poor Knights Islands, 201–183 m, 14 February 1974, R.V. *Acheron*, live juveniles (mostly brooded) with holotype and associated paratypes from behind outer lip rim of pagurid-inhabited shell of *Alcithoe larochei* (12, M.35374 on M.35369); 35°35.2'S, 175°45.6'E, Barrier Bank, NE of Great Barrier Island, 329–327 m, 25 January 1981, R.V. *Tangaroa*, empty shell (1, M.72069); 37°14.6'S, 176°51.0'E, Rangatira Knoll, NW of White Island, 407–162 m, 23 January 1981, R.V. *Tangaroa*, empty shell (1, M.74597); 37°00.8'S, 176°12.3'E, SE of Aldermen Island, alive, 178–248 m, 23 January 1979, R.V. *Tangaroa* (3, M.66657); 37°33.8'S, 176°59.0'E, Rungapapa Knoll, W of White Island, 188–228 m, 20 January 1979, R.V. *Tangaroa*, empty shell (1, M.64851).

Distribution (Figure 65): Eastern Northland southward to The Snares, New Zealand, living at 178–587 m.

Habitat: On living or pagurid-inhabited gastropod shells, usually behind outer lip rim, 178–587 m.

Remarks: *Grandicrepidula collinae* is immediately distinguishable from other crepiduliform species from the New Zealand region by the relatively huge but weakly delineated protoconch, the lack of a coiling suture on the protoconch, the lack of a muscle and muscle scar on the left side, and by the smooth, oblique, highly arched shell.

Grandicrepidula collinae is notable for the exceptionally large size of the brooded young (length up to 5.10 mm). Like other crepiduliform species, it is a protandrous hermaphrodite: the small male, occasionally bearing a yet smaller male, typically living attached to the dorsum of the larger female.

Etymology: After Rachel Collin (University of Chicago), in appreciation of her outstanding contributions to calyptraeid biology.

Genus *Sigapatella* Lesson, 1830

Sigapatella Lesson, 1830:389. Type species (by subsequent designation of Gray, 1847:157): *Calyptraea (Sigapatella) novaezealandiae* Lesson, 1830; Recent, New Zealand.

Zegalerus Finlay, 1926:392. Type species (by original designation): *Clypeola tenuis* Gray, 1867; Recent, New Zealand.

Diagnosis: Shell helical, septal rim broadly and evenly concave.

Remarks: Most recent authors have considered the type species of *Sigapatella* to be *Trochus calyptraeiformis* Lamarck, 1822 (Recent, Australia) by subsequent designation of Dall (1909). That species, however, was not among the species originally included there by Lesson

(1830), namely *Calyptraea novaezealandiae* Lesson, 1830, and *C. scutum* Lesson, 1830. The earliest valid and unequivocal subsequent designation of a type species (*C. novaezealandiae*) appears to be that of Gray (1847).

Bandel & Riedel (1994) interpreted *Sigapatella* as a synonym of *Calyptraea* Lamarck, 1799 (type species *Patella chinensis* Linnaeus, 1758; Recent, Europe), but *S. novaezealandiae* and other species discussed herein differ collectively from *C. chinensis* in that the septum edge is broadly and evenly concave instead of sigmoidal. Moreover, phylogenetic radiation of *Sigapatella* within the Australasian region was probably long independent from that of northern hemisphere-centered *Calyptraea*, so it seems appropriate to treat them as distinct genera.

Wenz (1940), Bandel & Riedel (1994), Macpherson & Gabriel (1961), and Wilson (1993) considered *Clypeola tenuis* to be the type species of *Clypeola* Gray, 1867, with *Zegalerus* thus an absolute synonym of *Clypeola*. The type species of *Clypeola*, however, is *Trochita clypeolum* Reeve, 1859 (= *Calyptraea decipiens* Philippi, 1845; Recent, southern South America) by tautonymy (Rehder, 1943). *Trochita clypeolum* has a convex septum rim and (typically) radial ribs at the periphery, and is referable to *Trochita* Schumacher, 1817 (type species *Trochus spiralis* Schumacher, 1817 = *Turbo trochiformis* Born, 1778; Recent, South America) (Powell, 1951, 1960).

Sigapatella novaezealandiae (Lesson, 1830)

(Figures 37, 40, 61, 72, 74, 75)

Zorn, 1778: No. 25, 69 (not binomial).

Calyptraea (Sigapatella) novaezealandiae Lesson, 1830:395; Thiele, 1929:248.

Crepidula maculata Quoy & Gaimard, 1835:422, pl. 72, figs. 6–9.

Calyptraea dilatata.—Gray, 1835:308; Gray, 1843:243 (not G. B. Sowerby I, 1825).

Calyptraea maculata.—Deshayes & Milne-Edwards, 1836: 628.

Trochita maculata.—Reeve, 1859b: *Trochita* pl. 3, fig. 15; Martens, 1873:28.

Calyptraea maculata.—Hutton, 1873:31; Suter, 1904:79.

Trochita novaezealandiae.—Hutton, 1878:30; Sowerby, 1883:63, pl. 450, figs. 87, 88.

Trochita novaezealandiae [sic].—Hutton, 1880:86.

Calyptraea (Sigapatella) calyptraeiformis [sic].—Tryon, 1886:122 (in part not Lamarck, 1822), pl. 35, fig. 99 only.

Calyptraea calyptraeiformis "Linn.".—Hutton, 1893:61 (not Lamarck, 1822).

Calyptraea inflata Hutton, 1893:61, pl. 7, fig. 58.

Calyptraea novaezealandiae [sic].—Suter, 1906:326.

Calyptraea (Sigapatella) maculata.—Suter, 1913:285, pl. 14, figs. 3, 3a.

Calyptraea (Sigapatella) maculata inflata.—Suter, 1915:9.

Calyptraea novaezealandiae.—Iredale, 1915:456; Riedel, 2000:45, text fig. 36, pl. 2, figs. 1, 2, pl. 8, fig. 13.

Sigapatella novaezealandiae.—Smith, 1915:82; Finlay, 1926: 392; Powell, 1937:73, pl. 10, fig. 25; Powell, 1946:75, pl. 10, fig. 25; Powell, 1955:94; Powell, 1957:99, pl.

10, fig. 25; Boshier, 1960:396; Powell, 1962:92, pl. 10, fig. 25; Grant-Mackie & Chapman-Smith, 1971:669; Pilkington, 1974:419, figs. 5A–D; Powell, 1976:95, pl. 17, fig. 25; Powell, 1979:148, pl. 30, fig. 5.

Calyptraea (Sigapatella) novozelandiae [sic].—Wenz, 1940:900, fig. 2648.

Calyptraea novaezelandia [sic].—Bandel & Riedel, 1994:339.

Description: Shell adequately described by Suter (1913:285), and Powell (1979:148). Radula (Figures 74, 75): cutting areas of central and lateral teeth broadly angulate with small terminal cusps; numerous small cusps on outer edges of lateral teeth.

Type data: *Calyptraea novaezelandiae*: presumed lost (not at MNHN); “Nouvelle-Zélande.” *Crepidula maculata*: presumed lost (not at MNHN). *Calyptraea inflata*: repository unknown, presumed lost; “Wanganui,” Castlecliffian (Middle Pleistocene).

Other material examined: *Fossil*—Shellbed N bank of Mangahao River, 1.6 km S of Mangahao, N Wairarapa (T24/462805), 1972, B. A. Marshall & M. B. Willoughby, Late Pliocene or Early Pleistocene (Nukumaruan). *Recent*—several thousand specimens (230 lots NMNZ) from throughout the geographic and bathymetric range.

Distribution (Figure 72): Late Pliocene or Early Pleistocene (Nukumaruan) to Recent. North, South, Stewart, Snares, Auckland and Chatham islands, New Zealand, 0–420 m; living intertidally to 220 m.

Habitat: Attached to hard substrata, 0–220 m.

Remarks: This common, widely known, widely distributed species is highly distinctive among New Zealand calyptraeids in the combination of rather strongly off-centered apex, large size (adults typically about 30 mm wide; rarely up to 42 mm—Wellington Harbour, M.15343), well defined spiral grooves on the first half teleoconch whorl; thick, hairy periostracum; and large, deeply perspective false umbilicus. Larval development is direct (Pilkington, 1974), the protoconch being paucispiral with a broad start (Figure 61). Among New Zealand *Sigapatella* species, the radula (Figures 74, 75) is distinctive in that the cutting areas of the central and lateral teeth are broadly angulate with small terminal cusps, and in that there are numerous small cusps on the outer edges of the lateral teeth.

Sigapatella terraenovae Peile, 1924

(Figures 38, 39, 41, 59, 60, 73, 77)

Trochita alta Hutton, 1885:329 (not Conrad *in* Wailes, 1854).

Calyptraea alta.—Hutton, 1893:62, pl. 7, fig. 59; Suter, 1915:8.

Calyptraea (Calyptropsis) alta.—Suter, 1906:326.

Calyptraea alta.—Suter, 1913:284, pl. 44, fig. 2.

Sigapatella calyptraeiformis.—Smith, 1915:83; Eales, 1923:18, figs. 16–19 (not Lamarck, 1822).

Sigapatella terraenovae Peile, 1924:22, text fig. 1; Mestayer, 1928:622 (in part: figs. 4–6 = *S. spadicea* Boshier, 1961), figs. 1–3 only; Finlay, 1926:391 (in part = *S. spadicea*); Dell, 1956:70.

Zegalerus crater Finlay, 1926:392 (replacement name for *T. alta* Hutton, 1885, not Conrad *in* Wailes, 1854). **New synonym.**

Zegalerus tumens Finlay, 1930:231; Marwick, 1948:30 (in part = *S. sp. aff. spadicea*), pl. 6, figs. 10, 11.

Zegalerus terraenovae.—Dell, 1956:70; Powell, 1979:149, pl. 30, figs. 8, 9.

Description: Shell adequately described by Peile (1924:22) and Powell (1979:149). Animal described by Eales (1923:18—as *S. calyptraeiformis*). Radula (Figure 77): leading cutting edges of lateral teeth almost straight and almost horizontal relative to longitudinal axis of radular ribbon; terminal cusp on central teeth small, broadly angulate; terminal cusp of lateral teeth broadly angulate with broad, smooth leading edge.

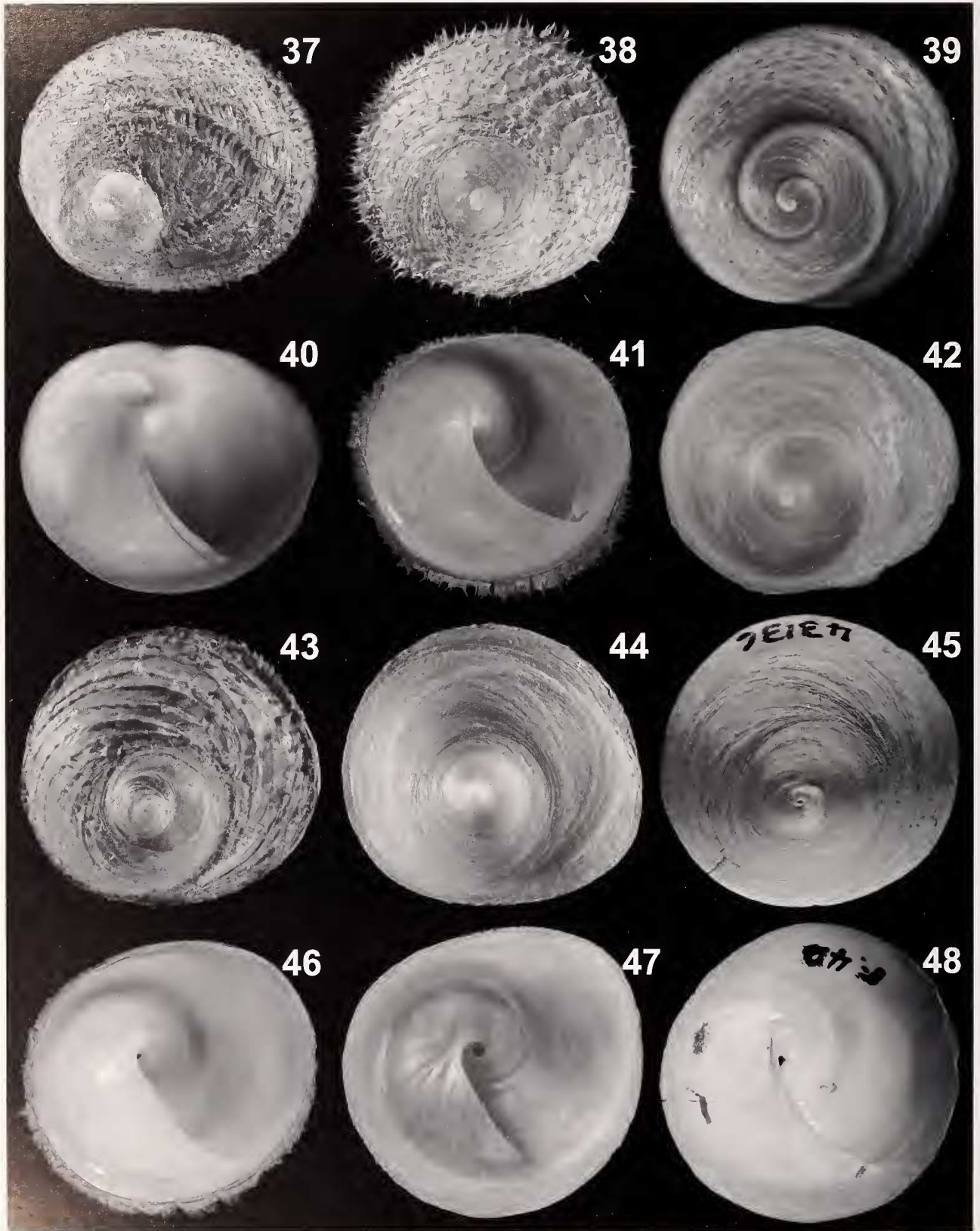
Type data: *Sigapatella terraenovae* lectotype (“holotype” Mestayer, 1928, fig. 1) BMNH 1924.3.18.9, and 17 paralectotypes (BMNH): 1924.3.18.10–11 (2), 1915.4.18.236–9 (4), 1977.157 (1), 1925.1.16.190–201 (10); off Spirits Bay, N North Island, New Zealand, 20–37 m. *Trochita alta* (= *Z. crater*): type material not traced and probably no longer extant; “Shrimpton’s” = Kikowheru Creek, W of Hastings, Hawkes Bay, North Island, New Zealand, Late Pliocene or Early Pleistocene (Nukumaruan). *Zegalerus tumens*: holotype AIM 70871; Cape Maria van Diemen, N North Island, New Zealand, beach.

Other material examined: *Fossil*—Shellbed N bank of Mangahao River, 1.6 km S of Mangahao, N Wairarapa (T24/462805), 1972, B. A. Marshall & M. B. Willoughby, Late Pliocene or Early Pleistocene (Nukumaruan) (32, M.42649); Tainui Shellbed (“Fleming Cu3”), Wanganui, 1924, W. R. B. Oliver, Middle Pleistocene (Castlecliffian) (1, M.151068). *Recent*—several hundred specimens (56 lots NMNZ) from throughout the geographic and bathymetric range.

Distribution (Figure 73): Nukumaruan (Late Pliocene or Early Pleistocene) to Recent. Off Three Kings Islands, northern tip of Northland, and Ranfurly Bank, East Cape, N North Island, New Zealand, 0–622 m; taken alive at 27–93 m.

Habitat: Attached to hard substrata, 27–93 m.

Remarks: *Sigapatella terraenovae* is rendered distinctive among Recent calyptraeids of the New Zealand region by the combination of thick, hairy periostracum, moderately subcentral apex, well defined spiral striae on the first half teleoconch whorl, and the narrowly constricted false umbilicus. Judging from the paucispiral protoconch and very wide start (330–470 μm) (Figures 59, 60), larval development is direct. Among New Zealand *Sigapatella* spe-



cies, the radula (Figure 77) is distinctive in that the leading cutting edges of the lateral teeth are almost straight and almost horizontal relative to the longitudinal axis of the ribbon, the terminal cusp on the central teeth is small and broadly angulate, and the terminal cusp of the lateral teeth is broadly angulate with a broad, smooth leading edge.

Specimens from northern Northland and the Three Kings Islands and Ranfurly Bank, East Cape are indistinguishable in shell and radular morphology and external anatomy. Since larval development is undoubtedly non-planktotrophic, it is quite possible that the northern and southern populations are fully isolated and relictual, perhaps dating from the last glacial maximum, when *S. terraenovae* was more widely distributed off the North Island: the places where it thrives today are areas of cool upwelling. Essentially similar distribution patterns are shown by a few other mollusks, such as the chiton *Parachiton textilis* Powell, 1937 (2 adult specimens from off Motiti Island, 20 m, M.152602), and the trochid *Calliostoma penniketi* Marshall, 1995, which are well represented off Spirits Bay and East Cape but, respectively, very rare or absent from intermediate localities (material NMNZ).

Zegalerus crater has been recorded as occurring Recent at the Chatham Islands, on the basis of a few worn beach shells, all of which examined appear to be reworked fossils, presumably originating from Nukumaruan beds at Titirangi, where it is common (Marwick, 1928). The status of the Chatham Islands species remains to be established.

Waipiian (middle Pliocene) specimens from Otahuhu brewery bore identified as *Zegalerus tumens* by Marwick (1948) have smaller protoconchs than *S. terraenovae* and lack spiral grooves on the first teleoconch whorl. They represent a distinct species of *Sigapatella* in which the start of the protoconch is markedly broader than in both *S. tenuis* and *S. spadicea*.

Suter (1915:8) stated that the "holotype" of *C. alta* "appears to be lost," and redescribed the species using "heutotypes" (literally meaning type specimens having the ascribed characteristics of another) from Petane, north of Napier. These same specimens are not "lectotype" and "paralectotype" as listed by Bradshaw et al. (1992), because they are not syntypes, *T. alta* having been based on material from Kikowheru Creek, west of Hastings (the

locality formerly otherwise known as Shrimpton's). Moreover, no Hutton specimens labeled *Trochita alta* from Kikowheru Creek have been located in New Zealand collections known to or likely to contain Hutton material, including Canterbury Museum, Christchurch, the most likely repository (N. Hiller, personal communication). Both Canterbury Museum "heutotypes" have very worn protoconchs, so it is clear that Suter's (1915) and Finlay's (1926:393) descriptions of the protoconch are based on other specimens, quite likely of other species and from other localities. Nevertheless, enough remains of the protoconch suture of the smaller specimen (M-2981) to indicate that its start was as broad as in contemporaneous specimens from Mangahao River. Since the latter are indistinguishable from Recent *S. terraenovae*, *C. alta* (= *Z. crater*) is confidently interpreted as a synonym.

Sigapatella ohopeana Marshall, sp. nov.

(Figures 45, 48)

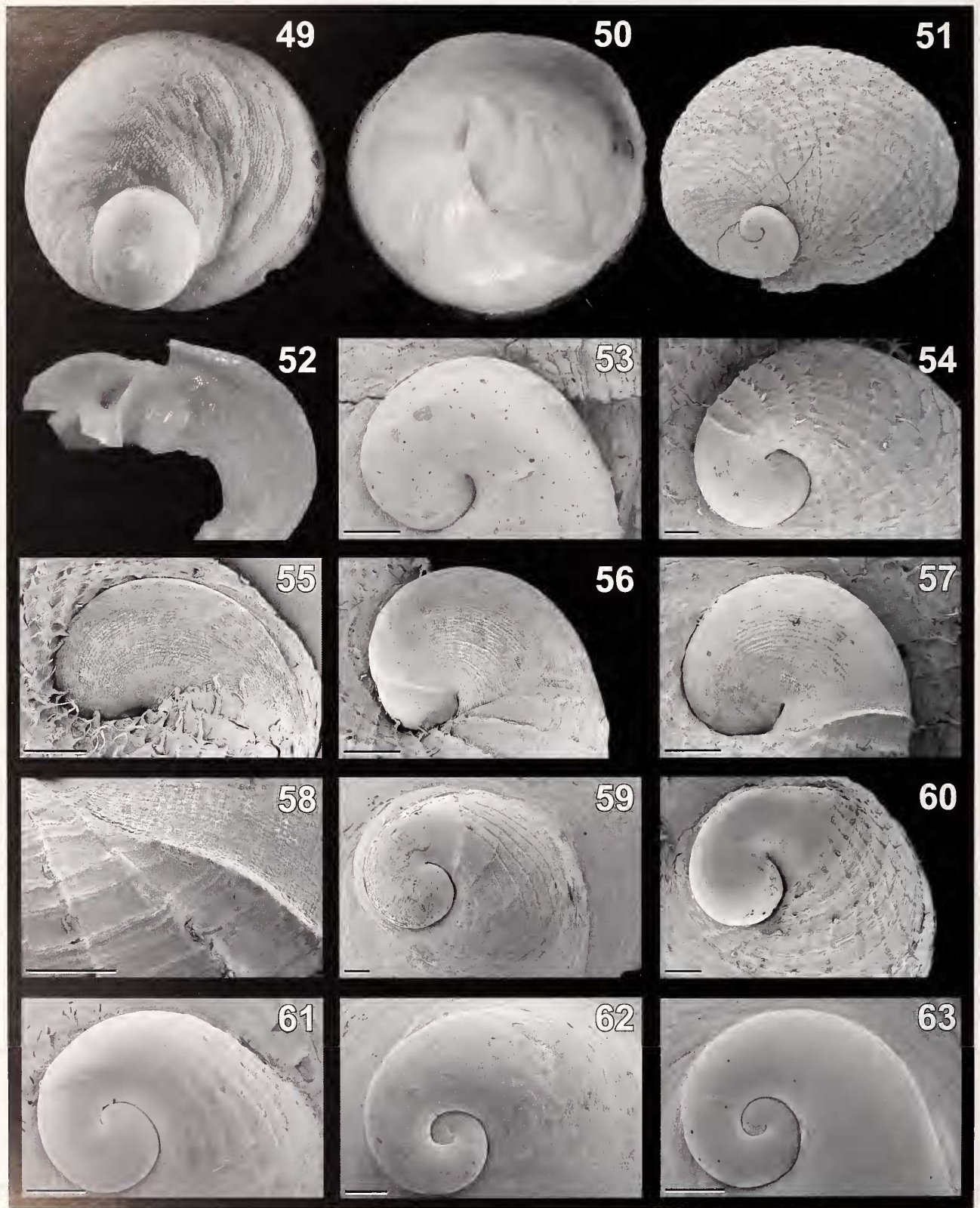
Diagnosis: Protoconch 230–260 μm wide, shell otherwise similar to that of *S. terraenovae*.

Description: Shell up to 23 mm wide, depressed-conical. Protoconch 700 μm wide, c. 0.4 smooth convex whorl, start 230–260 μm wide (development non-planktotrophic). First third of first teleoconch whorl strongly convex, subsequent whorls weakly convex. Low rounded spiral cords each with incised spiral groove at summit commence when shell 1.1 mm wide, weakening and vanishing at end of first half whorl. Subsequent whorls sculptured with irregular collabral growth lines, last half whorl with addition of traces of low, rounded spiral cords that accelerate outward more rapidly than generating curve. Septum weakly convex, rim broadly and evenly concave, modestly thickened at inner insertion and forming narrow, shallow, false umbilicus.

Type data: Holotype NZGS TM 8225, 6 paratypes M.43136; below old reservoir in stream at foot of Ohope-Whakatane road, Ohope Beach, (W15/644519), N North Island, New Zealand, 1970–1971, B. A. Marshall, shell-beds and blue muddy siltstone, Middle Pleistocene (Castlecliffian). Paratypes: large bend on Burma Road, between Whakatane and Ohope (W15/638502), 1960–1962,

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Figures 37–48. Shells of *Sigapatella* species. Figures 37, 40. *Sigapatella novaezelandiae* (Lesson, 1830), main channel, Whangaroa Harbour, 9–15 m, width 24 mm (M.35334). Figures 38, 39, 41. *Sigapatella terraenovae* (Piele, 1924), off Spirits Bay, 32 m, widths: 20.5 mm (38), 20.2 mm (39, periostracum removed), 21.4 mm (41) (M.150926). Figure 42. *Sigapatella spadicea* Boshier, 1961, periostracum removed, Otanerau, Queen Charlotte Sound, 20–29 m, width 17 mm (M.50816). Figures 43, 46. *Sigapatella spadicea*, off shelf inside Farewell Spit, 24–26 m, width 18.7 mm (M.49998). Figures 44, 47. *Sigapatella tenuis* (Gray, 1867), Titirangi Bay, Guards Bay, Marlborough, 18–22 m, width 17.2 mm (M.52389). Figures 45, 48. *Sigapatella ohopeana* Marshall, sp. nov., holotype, Ohope Beach, Late Pleistocene (Castlecliffian), width 15.6 mm (NZGS TM 8225).



B.A. Marshall, brown siltstone, Castlecliffian (2, M.96406).

Distribution: Middle Pleistocene (Castlecliffian), Ohope Beach, Bay of Plenty, N North Island, New Zealand.

Remarks: *Sigapatella ohopeana* closely resembles *S. terraenovae* in gross shell facies, including the presence of spiral grooves on the first teleoconch whorl, but differs principally in that the start of the protoconch in all type specimens is considerably narrower (width 230–260 μm as against 330–470 μm) than in any specimen of *S. terraenovae*. Judging from differences in protoconch morphology, development was non-planktotrophic rather than planktotrophic as in *S. tenuis* and *S. spadicea*. Given that *S. terraenovae* evidently dates to the Late Pliocene or early Pleistocene, *S. ohopeana* seems unlikely to be a form of that species undergoing progressive enlargement of the first protoconch whorl over time.

Etymology: From the Maori place name Ohope, the type locality.

Sigapatella superstes Fleming, 1958

(Figures 49, 50, 54, 57, 58, 76, 80)

Sigapatella superstes Fleming, 1958:141, figs. 1–4; Powell, 1979:148, pl. 30, fig. 10.

Description: Shell adequately described by Fleming (1958:141) and Powell (1979:148). Radula (Figure 76): most similar to that of *S. novaezelandiae*, but terminal cusps on central and lateral teeth much larger, and secondary cusps on outer edges of laterals larger.

Type data: Holotype NMNZ M.129; Cape Maria van Diemen, N North Island, New Zealand, beach.

Other material examined: 33°57.0'S, 172°19.0'E, King Bank, N of Three Kings Islands, 128 m, 1 February 1981, R.V. *Tangaroa* (3, M.151038); 33°57.0'S, 171°45.4'E, Middlesex Bank, NW of Three Kings Islands, 98–103 m, 31 January 1981, R.V. *Tangaroa* (1, M.151191); 33°57.4'S, 172°19.4'E, King Bank, 128–123 m, 1 February

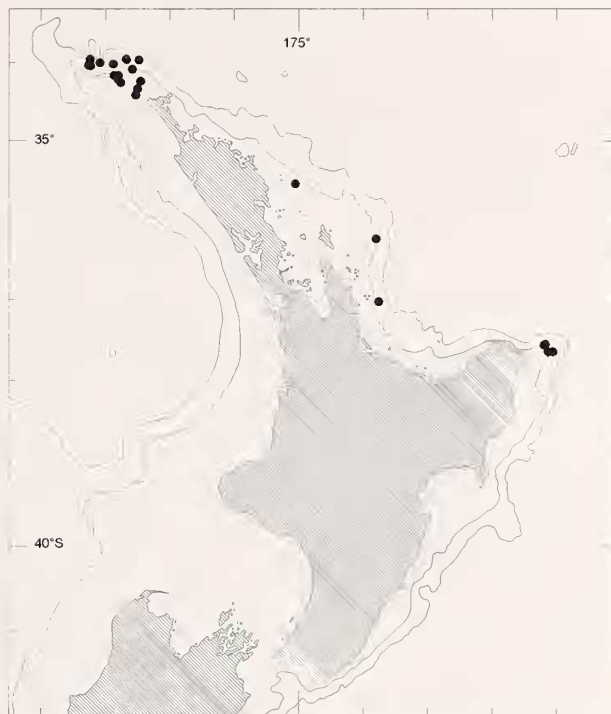


Figure 64. Distribution of *Maoricrypta kopua* Marshall, sp. nov., off North Island, New Zealand (200 and 1000 m isobaths indicated).

1981, R.V. *Tangaroa* (17, M.100503); 33°58.0'S, 172°30.6'E, 37 km NE of Great Island, Three Kings Islands, 550 m, 25 June 1978, R.V. *Tangaroa* (3, M.151037); 34°00'S, 171°55'E, Three Kings Trough, 805 m, 15 July 1962, R.N.Z.F.A. *Tui* (2, M.20813); 34°06.5'S, 172°04.7'E, 11 km NW of Great Island, 310 m, 30 June 1978, R.V. *Tangaroa* (3, M.151042); 34°08.5'S, 172°11'E, off Northeast Island, Three Kings Islands, 102 m, 18 February 1974, R.V. *Acheron* (5, M.34418); 34°09'S, 172°10'E, reef between Great Island and Farmer Rocks, 33 m, 17 February 1986, scuba, G. S. Hardy (5, M.93955); 34°09.5'S, 172°08.8'E, Southeast Bay, Great Island, alive under boul-

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Figures 49–63. Shells of *Sigapatella* species. Figure 49. *Sigapatella superstes* Fleming, 1948, off Three Kings Islands, 91 m, width 23.2 mm (M.33764). Figure 50. *S. superstes*, between Pandora Bank and Cape Maria van Diemen, 38–43 m, width 20.5 mm (M.81145). Figures 51, 53. *Sigapatella nukumaruaana* Marshall, sp. nov., subadult holotype, Mangahao, Wairarapa, Late Pliocene or Early Pleistocene (Nukumaruan), width 5.70 mm (NZGS TM 8226). Figure 52. *S. nukumaruaana*, fragmentary adult paratype, Mangahao, Wairarapa, Late Pliocene or Early Pleistocene (Nukumaruan), width 25 mm (M.42647). Figures 54, 57, 58. *Sigapatella superstes*, Southeast Bay, Three Kings Islands, 20–22 m (M.134706). Figure 55. *Sigapatella superstes*, off Ruamahua-nui Island, Aldermen Islands, 38 m (M.112746). Figure 56. *Sigapatella superstes*, reef between Great Island and Farmer Rocks, Three Kings Islands, 33 m (M.93955). Figure 59. *Sigapatella terraenovae* (Piele, 1924), off Three Kings Islands, 91 m (M.33765). Figure 60. *Sigapatella terraenovae*, off Cape Reinga, 78 m (M.151043). Figure 61. *Sigapatella novaezelandiae* (Lesson, 1830), Whangaroa Harbour entrance, 25 m (M.151547). Figure 62. *Sigapatella spadicea* Boshier, 1961, off Manawatu River mouth, 86 m (M.53848). Figure 63. *Sigapatella tenuis* (Gray, 1867), Deep Water Cove, Bay of Islands, 23–32 m (M.95485). Scale bar 58 = 100 μm , others = 200 μm .

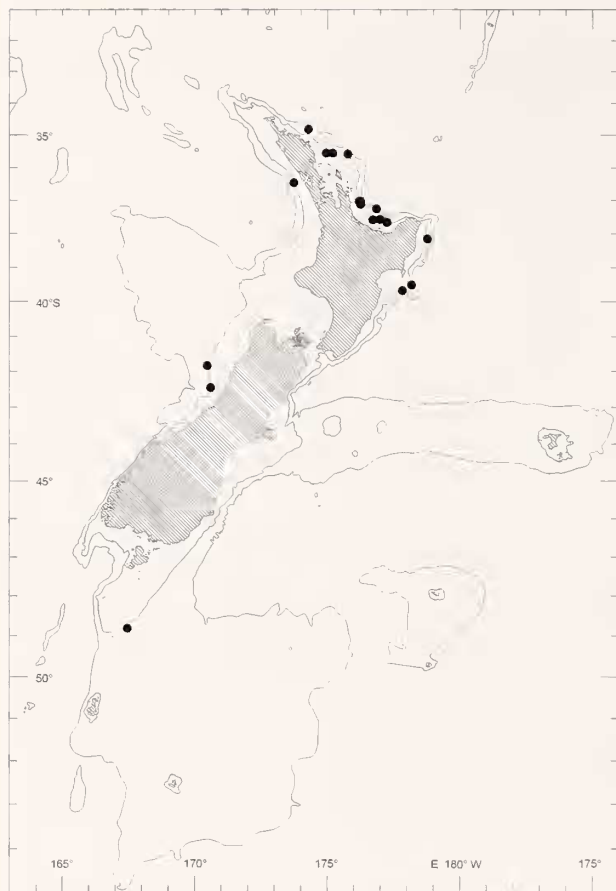


Figure 65. Distribution of *Grandicrepidula collinae* Marshall, sp. nov., off New Zealand (200 and 1000 m isobaths indicated).

ders. 13–15 m, 5 March 1997, K. W. Burch & D. Crosby (2, M.134650); 34°09.5'S, 172°08.8'E, Southeast Bay, 20–22 m, 4 March 1997, K. Burch & D. Crosby (8, M.134706); Southeast Bay, 23 m, 16 February 1986, scuba, F. J. Brook (1, M.109398); 34°10.8'S, 172°02.6'E, off N face of Hinemoa Island, Three Kings Islands, 23 m, 11 February 1986, scuba, G. S. Hardy (1, M.112572); 34°11'S, 172°03'E, off West Island, Three Kings Islands, *Elingamite* wreck, 37 m, 16 March 1981, K. Tarlton (1, M.151039); 34°11'S, 172°10'E, off Three Kings Islands, 91 m, 19 February 1974, R.V. *Acheron* (1, M.33764); 34°14.1'S, 172°09.0'E, S of Great Island, 192–202 m, 1 February 1981, R.V. *Tangaroa* (3, M.151040); 34°22.8'S, 172°24.6'E, NW of Cape Reinga, 121 m, 2 February 1981, R.V. *Tangaroa* (1, M.151041); 34°29.4'S, 172°35.2'E, between Pandora Bank and Cape Maria van Diemen, 38–43 m, 3 February 1981, R.V. *Tangaroa* (1, M.81145); 34°29.8'S, 172°35.4'E, between Pandora Bank and Cape Maria van Diemen, 38–43 m, 3 February 1981, R.V. *Tangaroa* (1, M.70947); Cape Maria van Diemen, beach, August 1976, P. R. Jamieson (2, M.111077); Cape Maria van Diemen, beach, 29 August 1957, A. W. B. Powell (1,

M.13030); 34°42.8'S, 173°14.5'E, off Rangaunu Bay, 63 m, 27 January 1981, R.V. *Tangaroa* (7, M.151192); 36°57.2'S, 176°05.8'E, off E side of Ruamahua-nui Island, Aldermen Islands, 38 m, 30 November 1987, scuba, G. S. Hardy (1 very fresh juvenile, M.112746).

Distribution (Figure 80): Off Three Kings Islands and off N tip of North Island, New Zealand (1 juvenile off Aldermen Islands), 0–805 m; taken alive (1 station) at 13–15 m.

Habitat: Attached to hard substrata, 13–15 m.

Remarks: Among Recent *Sigapatella* species, *S. superstes* is extremely distinctive in its teleoconch sculpture of sharply incised, irregularly wavy spiral grooves and com-marginal grooves that intersect to form a granular pattern. The paucispiral protoconch with wide start indicates non-planktotrophic larval development. That development may be lecithotrophic is suggested by the occurrence of a juvenile specimen off the Aldermen Islands, which presumably originated from self recruiting populations off northern Northland. The radula (Figure 76) is distinctive in that the terminal cusps on the central and lateral teeth are large and broadly angulate. Among New Zealand *Sigapatella* species, the radula is most similar to that of *S. novaezelandiae*, but the terminal cusps on the central and lateral teeth are much larger, and the secondary cusps on the outer edges of the laterals are larger.

A similar species of Late Pliocene or Early Pleistocene age is described below.

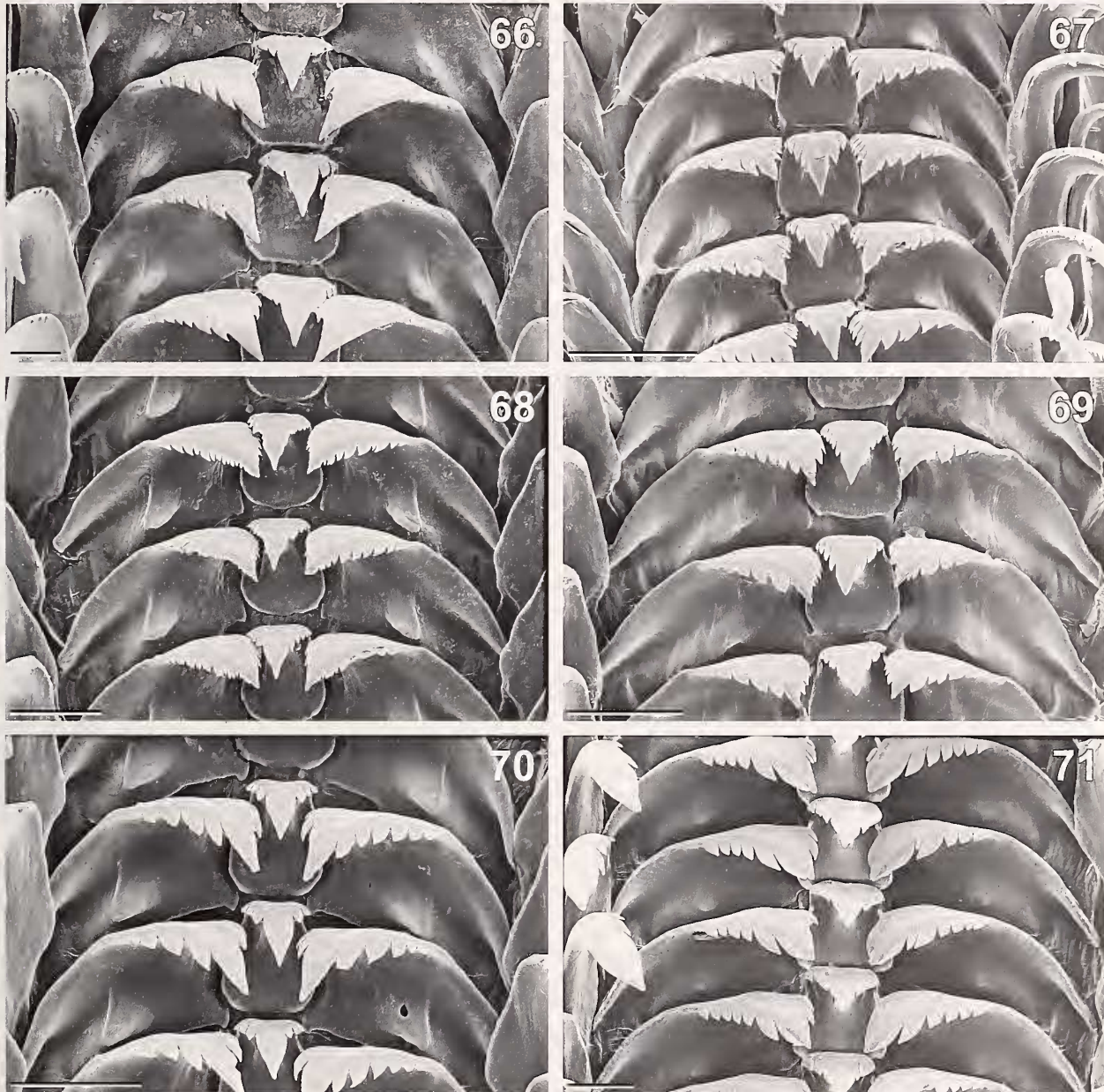
Sigapatella nukumarua Marshall, sp. nov.

(Figures 51–53)

Diagnosis: Shell similar to that of *Sigapatella superstes* but with coarser teleoconch sculpture and larger false umbilicus.

Description: Shell up to ca. 22 mm wide, of moderate thickness, spire moderately elevated. Protoconch of 0.5 convex whorl, 800–830 μ m wide, finely spirally lirate, start broadly rounded (development non-planktotrophic). Teleoconch of up to 2.5 rather strongly and evenly convex, and rather regularly expanding whorls, suture well defined; spire sculptured throughout with sharply incised, irregular, wavy spiral grooves that intersect with com-marginal grooves to form pattern of coarse, rounded granules. Base excavate, septum weakly convex, rim broadly concave, false umbilicus large and deep.

Type data: Holotype NZGS TM 8226, 5 paratypes NMNZ M.42647; shellbed N bank of Mangahao River, 1.6 km S of Mangahao, N Wairarapa, S North Island, New Zealand, (T24/462805), 1972, B. A. Marshall and M. B. Willoughby, Late Pliocene or Early Pleistocene (Nukumaruan).



Figures 66–71. Radulae of *Maoricrypta* and *Grandicrepidula* species (adults). Figure 66. *Maoricrypta costata* (G. B. Sowerby I, 1824), Kokinga Point, Bay of Islands, intertidal (M.42098). Figure 67. *Maoricrypta monoxyta* (Lesson, 1830), Reef Point, Ahipara, intertidal (M.151210). Figure 68. *Maoricrypta sodalis* Marshall, sp. nov., paratype, off Cape Runaway, 27–72 m, M.65233. Figure 69. *Maoricrypta kopua* Marshall, sp. nov., paratype, off Aldermen Islands, 289–292 m (M.134083). Figure 70. *Maoricrypta youngi* Powell, 1940, off Cape Reinga, 88 m (M.36032). Figure 71. *Grandicrepidula collinae* Marshall, sp. nov., paratype, N of Mayor Island, 380–420 m (M.90205). Scale bars = 50 μ m.

Distribution: Late Pliocene-Early Pleistocene (Nukumaruan), Wairarapa, S North Island, New Zealand.

Remarks: *Sigapatella nukumaruana* resembles the recent species *S. superstes* in size and gross facies, but differs in having coarser teleoconch sculpture at all stages of growth, and in having a larger false umbilicus at equiv-

alent stages of growth. The holotype is a juvenile, all other specimens, including adults (Figure 52), being more or less fragmentary but otherwise very well preserved.

Etymology: After the Nukumaruan Stage (Late Pliocene-Early Pleistocene).



Figure 72. Distribution of *Sigapatella novaeseelandiae* (Lesson, 1830) off New Zealand (200 and 1000 m isobaths indicated).

Sigapatella spadicea Boshier, 1961

(Figures 42, 43, 46, 62, 78, 81)

Sigapatella terraenovae.—Mestayer, 1928:622 (in part not Peile, 1924), figs. 4–6 only; Finlay, 1926:391 (in part).
Zegalerus tenuis.—Dell, 1956:70; Powell, 1979:149 (in part).

Sigapatella spadicea Boshier, 1961:104, text fig. 1.

Description: (supplemental to that of Boshier 1961:104) Protoconch 770–870 μm wide, of 1.25 convex whorls, rapidly expanding from small nucleus (larval development probably planktotrophic). Radula (Figure 78): Central and lateral teeth with very acutely tapered cutting areas, each with large, long, slender terminal cusp. Central tooth with five or six sharp secondary cusps on each side. Lateral teeth each with four to six sharp cusps on outer edge, and four sharp cusps on inner edge.

Type data: Holotype NMNZ M.18089; trawled north of Kapiti Island, S North Island, New Zealand, 55 m, F. Abernethy.

Other material examined: *Fossil*—Shellbed N bank of



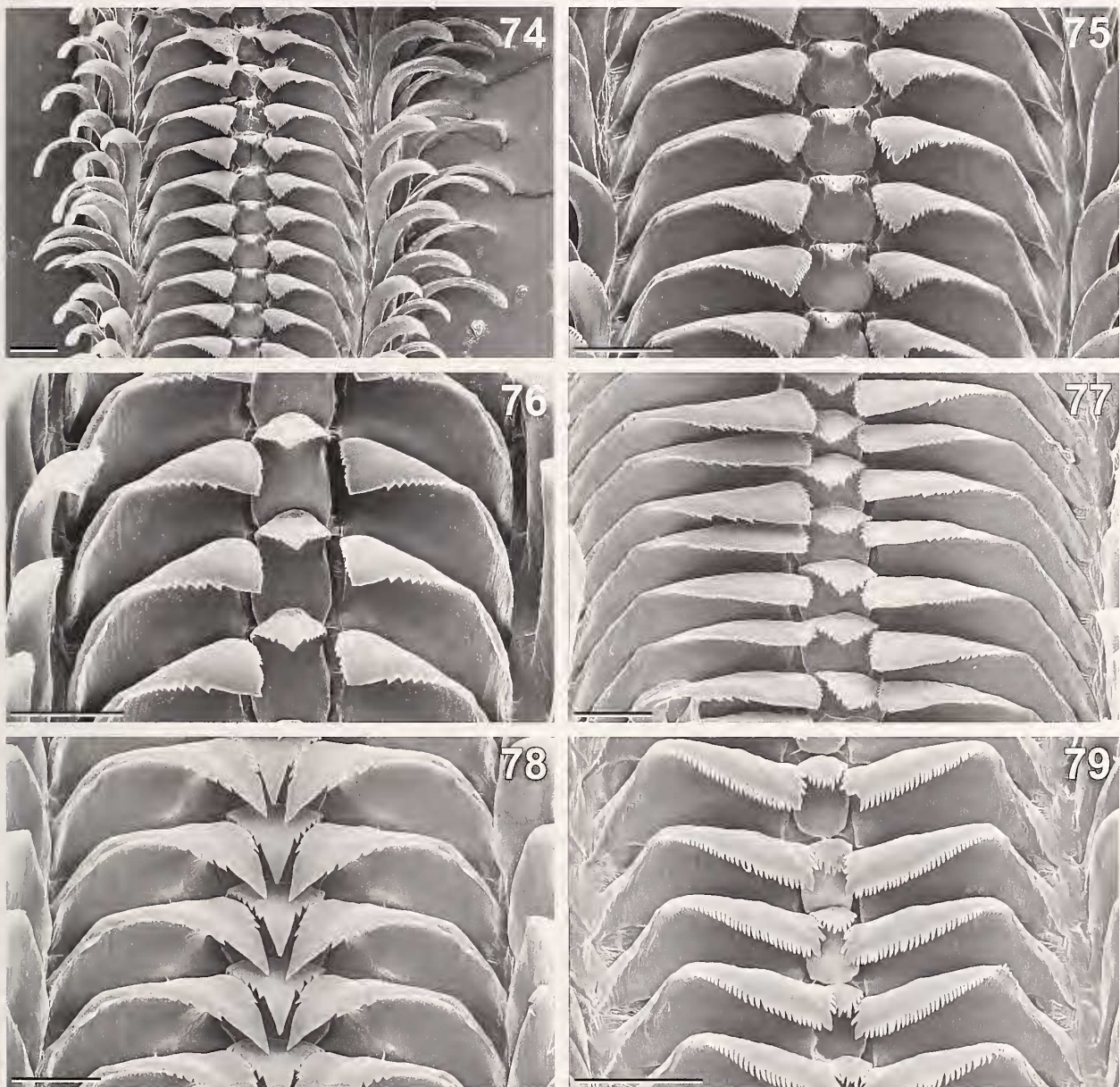
Figure 73. Distribution of *Sigapatella terraenovae* (Peile, 1924), off North Island, New Zealand (200 and 1000 m isobaths indicated).

Mangahao River, 1.6 km S of Mangahao, N Wairarapa (T24/462805), 1972, B. A. Marshall and M. B. Willoughby, Late Pliocene or Early Pleistocene (Nukumaruan); Landguard Bluff, Wanganui, 1909, W. R. B. Oliver, Pleistocene (Castlecliffian) (10, M.151067). *Recent*—> 1000 specimens (142 lots NMNZ) from throughout the geographic and bathymetric range.

Distribution (Figure 81): Late Pliocene or Early Pleistocene (Nukumaruan) to Recent. North, South, Stewart islands, New Zealand, 4–533 m; taken alive at 4–533 m.

Habitat: Attached to hard substrata (typically shells), 4–533 m.

Remarks: *Sigapatella spadicea* differs from the superficially similar, sympatric species *S. tenuis*, principally in lacking oblique spiral threads on the teleoconch, and in that the periostracum is prominently commarginally lamellate and spinose rather than smooth. The radula (Figure 78) differs markedly from those of other New Zealand *Sigapatella* species in having narrowly tapered cutting areas and large, narrowly tapered terminal cusps on the central and lateral teeth, more closely resembling those of *Maoricrypta* species in gross facies. The protoconch is extremely similar in both species, with a relatively narrow start, and about 1.25 whorls instead of about 0.5 whorl, suggesting planktotrophic larval development; it is unclear whether planktotrophic larvae described by Pilkington



Figures 74–79. Radulae of *Sigapatella* species (adults). Figures 74, 75. *Sigapatella novaezelandiae* (Lesson, 1830), Pukenui Wharf, Houhora Harbour (M.45067). Figure 76. *Sigapatella superstes* Fleming, 1948, Southeast Bay, Great Island, Three Kings Islands, 13–15 m (M.134650). Figure 77. *Sigapatella terraenovae* (Piele, 1924), off Spirits Bay, 40 m (M.148035). Figure 78. *Sigapatella spadicea* Boshier, 1961, Port Hardy, D’Urville Island, 18 m (M.54687). Figure 79. *Sigapatella tenuis* (Gray, 1867), Guards Bay, Marlborough Sounds, 18–22 m (M.52389). Scale bars = 50 μ m.

ton (1976) are of *S. tenuis* or *S. spadicea*, both of which occur in her study area. The fossil specimens are indistinguishable from Recent shells in all aspects of shell morphology.

Sigapatella tenuis (Gray, 1867)

(Figures 44, 47, 63, 79, 81)

Clypeola tenuis Gray, 1867:735.

Trochita tenuis.—Hutton, 1873a:32.

Trochita scutum.—Hutton, 1878:30; Hutton, 1880:86 (not Lesson, 1830).

Calyptraea scutum.—Suter, 1904:79; Suter, 1913:284, pl. 44, fig. 4 (not Lesson).

Calyptraea tenuis.—Hedley, 1913:289; Bandel & Riedel, 1994:340, pl. 7, figs. 4, 5 (in part = *S. hedleyi* E. A. Smith, 1915); Riedel, 2000:47, pl. 8, figs. 11, 12.

Sigapatella tenuis.—Smith, 1915:83, pl. 1, figs. 20–22; Eales, 1923:19.

Zegalerus tenuis.—Finlay, 1926:392; Powell, 1937:73, pl.



Figure 80. Distribution of *Sigapatella superstes* Fleming, 1948 off North Island, New Zealand (200 and 1000 m isobaths indicated).

10, fig. 24; Powell, 1946, pl. 10, fig. 24; Powell, 1957: 99, pl. 10, fig. 24; Powell, 1962:92, pl. 10, fig. 24; Powell, 1976:95, pl. 17, fig. 24; Powell, 1979:149 (in part = *S. spadicea* Boshier, 1961), pl. 30, figs. 6, 7.
Calyptraea (Clypeola) tenuis.—Thiele, 1929:248; Wenz, 1940:900, fig. 2650.
 NOT *Zegalerus tenuis*.—Dell, 1956:71 (= *S. spadicea*).

Description: Shell adequately described by Suter (1913: 284—as *Calyptraea scutum*). Radula (Figure 79) with numerous small slender cusps on the central and lateral teeth; outer cutting edge of each lateral tooth long, almost straight and oblique relative to the horizontal axis of the radular ribbon.

Type data: Syntypes (3) BMNH 1977151; New Zealand.

Other material examined: *Fossil*—Tainui Shellbed, Wanganui, 1924, W. R. B. Oliver, Castlecliffian (Middle Pleistocene) (16, M.27327); Landguard Bluff, Wanganui, 1909, W. R. B. Oliver, Late Pleistocene (Haweran) (35, M.16422); Te Piki road cutting, between Whangaparaoa and Te Araroa (Y14/561904), 1966–1969, B. A. Marshall, Haweran (3, M.40120). *Recent*—several thousand specimens (250 lots NMNZ) from throughout the geographic and bathymetric range.

Distribution (Figure 81): Late Pleistocene (Castlecliffian)—Recent. Three Kings, North, South, Stewart and

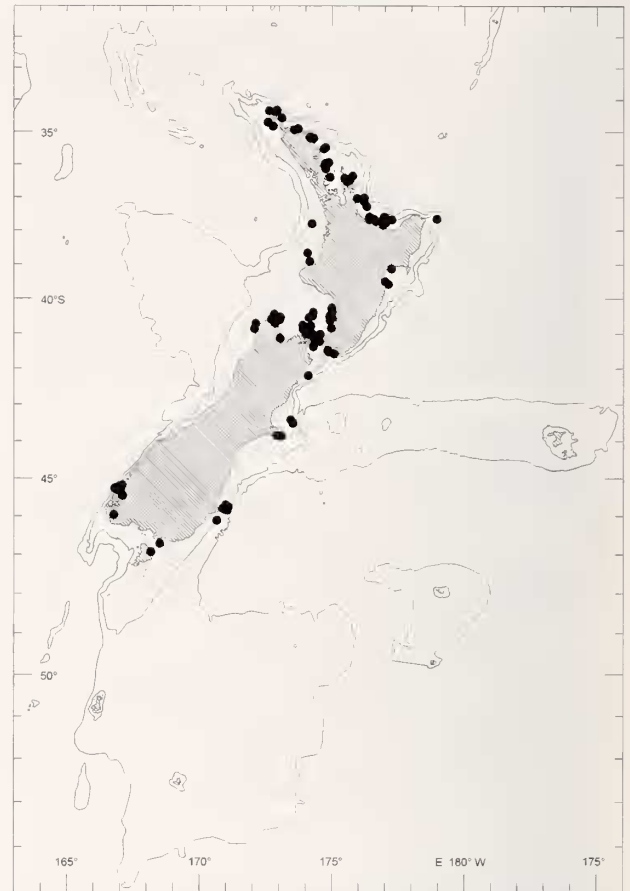


Figure 81. Distribution of *Sigapatella spadicea* Boshier, 1961, off New Zealand (200 and 1000 m isobaths indicated).

Chatham islands, New Zealand, 0–604 m; taken alive at 2–315 m.

Habitat: Attached to hard substrata, 2–315 m.

Remarks: The shell morphology of *Sigapatella tenuis* is distinctive among New Zealand *Sigapatella* species in the combination of protoconch of 1.25 smooth whorls with narrow start, outwardly curving spiral threads on the teleoconch, and the smooth periostracum. The radula is extremely distinctive in having small slender cusps on the central and lateral teeth, and in that the outer cutting edge of each lateral tooth is long, almost straight and oblique relative to the horizontal axis of the radular ribbon.

Clypeola tenuis Gray, 1867, is a secondary homonym of *Calyptraea (Calypeopsis) tenuis* Broderip, 1834, and no replacement name has been provided. There is no need to rename Gray's well known species, however, because Broderip's species belongs in *Crucibulum* Schumacher, 1817 (ICZN, 1999), perhaps a synonym of *C. lignarium* (Broderip, 1834) (Keen, 1971). Bandel & Riedel (1994) recorded *S. tenuis* from both New Zealand and New South Wales, apparently implying that the Australian spe-

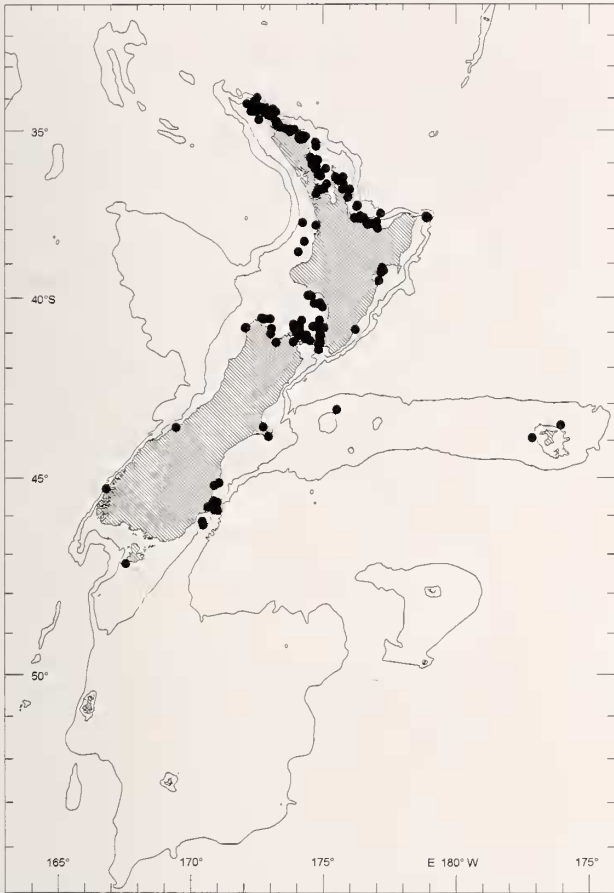


Figure 82. Distribution of *Sigapatella tenuis* (Gray, 1867), off New Zealand (200 and 1000 m isobaths indicated).

cies *S. hedleyi* (E. A. Smith, 1915) was a synonym of *S. tenuis*. This is not so, *S. hedleyi* differing from *S. tenuis* (principally) in that the start of the protoconch is much broader, indicating that larval development is non-planktotrophic rather than planktotrophic as in *S. tenuis*.

Since the larval shell seems to be indistinguishable from that of *S. spadicea*, it is unclear whether planktotrophic larvae described by Pilkington (1976) are of *S. tenuis* or *S. spadicea*.

The largest specimen examined (Wellington Harbour, M.40067) is 24 mm in diameter.

Key to New Zealand Recent Calyptraeidae

- 1. Shell slipper-shaped (crepiduliform) 2
- Shell not slipper-shaped (spiral) 7
- 2. Shell with strong radial sculpture
..... *Maoricrypta costata*
- Shell essentially smooth 3
- 3. Shell with one (right) muscle/scar beside insertion of septum *Grandicrepidula collinae*
- Shell with right and left muscles/scars beside insertion of septum 4

- 4. Shell white; strongly depressed protoconch not tilted relative to apertural plane 5
- Shell typically brownish, protoconch not depressed, somewhat tilted relative to apertural plane *Maoricrypta youngi*
- 5. Shell externally markedly convex, animal yellow (living outside living gastropods and mussels) ...
..... *Maoricrypta monoxyla*
- 6. Shell strongly flattened, animal whitish (living within apertures of pagurid-occupied gastropod shells) 6
- 7. Protoconch 2.8–3.9 mm long, crisply radially striate *Maoricrypta sodalis*
- Protoconch 3.9–5.0 mm long, weakly radially striate or smooth *Maoricrypta kopua*
- 8. Protoconch of more than 1 whorl, tip of apical fold narrow 8
- Protoconch of less than 1 whorl, tip of apical fold broad 9
- 9. Teleoconch with outwardly spiralling radial threads, periostracum smooth ... *Sigapatella tenuis*
- Teleoconch without radial threads, periostracum hairy or lamellar *Sigapatella spadicea*
- 10. Teleoconch covered with crisp, granular sculpture *Sigapatella superstes*
- Teleoconch without granular sculpture 10
- 11. Large false umbilicus .. *Sigapatella novaezelandiae*
- No false umbilicus *Sigapatella terraenovae*

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